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It is a pleasure to commend the far-sighted policy of the Office of Naval Research, with its emphasis on basic research, as a result of which a grant has made possible the continuation of the Coral Atoll Program of the Pacific Science Board.

It is of interest to note, historically, that much of the fundamental information on atolls of the Pacific was gathered by the U. S. Navy's South Pacific Exploring Expedition, over one hundred years ago, under the command of Captain Charles Wilkes. The continuing nature of such scientific interest by the Navy is shown by the support for the Pacific Science Board's research programs, CIMA, SIM, and ICCP, during the past five years. The Coral Atoll Program is a part of SIM.

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Editorial Staff

F. R. Fosberg, editor
M. H. Sachet, assistant editor

Correspondence concerning the Atoll Research Bulletin should be addressed to the above

c/o Pacific Science Board
National Research Council
2101 Constitution Avenue, N. W.
Washington 25, D.C., U.S.A.

THE INSECT LIFE OF ARNO 1/

by

R. L. Usinger and Ira La Rivers

On Arno, as elsewhere, insects are the most numerous of land animals. This well-known phenomenon is a function of their small size and their high reproductive potential. The total number of species of land anthropods on Arno is estimated at 500. This may be compared with 96 species reported from Canton Island (a somewhat drier coral atoll) and nearly 1000 recorded from Guam (a much larger, high island). The insects of Arno have to be abundant in order to maintain themselves, because most of the higher terrestrial animals live on them. Thus, insects are the first link in many of the food chains, such forms as aphids, plant bugs, caterpillars and, in fresh water, midge larvae acting as primary converters of green plants into animal food.

Of no less importance than the "grazers" are the ever-present ants and cockroaches which act as scavengers and the wood-boring beetles and termites which, with the help of bacteria and fungi, restore logs to humus. Other katabolic agents include the flies and beetles which play a dominant role in the decay of fallen fruits and others which perform a similar function in dung and carrion.

Not all insects are occupied in such vital jobs of a constructive or destructive nature. Analysis of the fauna reveals that a considerable proportion of the insects in any community are busily engaged in eating each

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1/ This report covers field work carried out in 1950 as part of the Coral Atoll Project of the National Research Council's Pacific Science Board. These studies were aided by a contract between the Office of Naval Research, Department of the Navy and the National Academy of Sciences (NR 160 175).

other. One-fourth of the insects of Arno fall directly in this category--as predators or parasites and the percentage may be even higher when careful rearing reveals the true numbers of entomophagous parasites. Then there are the small ectoparasites--the lice and mites, and one louse fly--which infest birds and rats.

Another vital though inconspicuous function of insects in most mainland areas is pollination. On Arno probably three-fifths of the higher plants are insect pollinated. Detailed studies on this are lacking but the single Arno bee, a leaf-cutting species of Megachile, collects pollen on its abdominal hairs. It nests in the dead twigs of Scaevola and visits various flowers including Triumfetta, Scaevola and Wedelia.

The above-mentioned activities are basic to any community of plants and animals and are quite independent of man. For this reason, the insects, with but few exceptions, are not much different on the uninhabited islets than in the villages. Furthermore, many of the insects undoubtedly arrived before the first natives and had achieved a state of equilibrium which may not have changed significantly with the advent of man.

There are a few important exceptions to this generalization--such as the house fly, the house mosquito, domestic cockroaches, and lice. The role of these and other insects associated with man will be discussed in detail later.

Animal Communities and Habitats

It is a well-known fact that plants and animals are discontinuously distributed over the earth's surface. Nevertheless it comes as a surprise to find that five square miles of practically level land of similar origin and relatively uniform composition should present such a variety of distinct

plant and animal associations. In spite of a superficial similarity there are at least four distinct terrestrial communities and numerous distinct but interrelated strata within each. In addition there is the marine habitat including tide pools and the open ocean which is inhabited by marine water striders.

Marine Insects. The virtual absence of the largest group of animals, the insects, from the largest habitat in the world, the ocean, has been the subject of much speculation (Buxton, 1926). It has been pointed out that insects of saline lakes can tolerate greater concentrations of salt than are found in the ocean, and insects of torrential streams and waterfalls are subjected to conditions which are comparable to wave action. What, then, are the limiting factors that prevent insects as a group from colonizing the sea? The answer is to be found in the ancestry of insects, in the fact that they evolved a special breathing mechanism (tracheae) which was admirably suited to terrestrial life and only secondarily adaptable to life in the water. But perhaps the most critical factor of all is the depth of the ocean, for deep water is uninhabitable even to fresh water forms, the profundal bottom habitat of our deepest lakes being beyond the reach of insects. Then there is the fact that the ocean is already occupied by another group of Arthropods, the Crustacea. This group, which includes the shrimps, crabs and their relatives, is so perfectly adapted to all of the available niches in the sea that would-be invaders such as insects cannot compete with them.

One group of insects has overcome the above difficulties by occupying the surface of the ocean. The marine water striders attracted the attention of early voyagers who found small, gray, long-legged creatures coursing about on the high seas. These marine forms differ from their fresh-water relatives

in that they have permanently lost their wings, there being no need to utilize this means of dispersal in the ocean which, unlike fresh-water ponds, is in no immediate danger of drying up.

Halobates micans lives in the open ocean and in the deep parts of the lagoon at Arno. Nymphs and adults are blown up on the beach by strong winds. This happened on the beach of the lagoon at Ine Village one afternoon and evening. The bugs were awkward on land and sought shelter from the wind in the smallest depressions or in footprints on the beach. Here they doubtless fell easy prey to a golden plover which patrolled that section of beach and also to the ghost crabs which glided swiftly over the sand after dark.

In protected coves such as are found on the ocean side of Tagelib and in the lagoon at the north horn of the atoll two other marine water striders are found. One of these, Halobates mariannarum, differs only slightly from its relatives in the Marianas and Carolines, but the fact that it differs at all suggests that it is endemic to the reefs of the Marshalls and has been isolated for a long time. Nymphs and adults of this local Halobates swim in groups of hundreds or thousands in shallow water. A search was made for the plankton which must serve as their food, but to no avail. Presumably, they feed on plankters which rise to the surface at night. The fact that Halobates are not eaten by fish suggests that the median metasternal scent gland repels the ever-present marine predators or, perhaps, makes the bugs distasteful to the fish.

Even more local, in small embayments, is Halovelia, a marine water strider whose body is less than one-twelfth of an inch in length. The male is even smaller and rides on the back of the female to insure that the sexes will not be separated by wind or tide.

The Strand. In the daytime the beaches of Arno are clean and support very few insects. Robber flies flash here and there, capturing mostly flies, but this is about the extent of the activity over the uninterrupted stretches of sand.

At night, Arno beaches take on a changed aspect. The Ghost crabs (Ocypode ceratophthalma), common enough during daylight hours, literally swarm over the sands after dark. They dart everywhere. At first, the insect fauna seems to be poorly represented, few species coming to lights, and then usually only one or two individuals of any given kind. As a consequence, the discovery, one night, of a small, white cricket marching about the beaches in great numbers came as somewhat of a surprise. They were particularly abundant at low tides when the greatest expanse of beach was exposed, and seemed to be coming from everywhere. They ranged in size from the quarter-inch adults down to barely visible early instar nymphs, all marching sedately by the coleman lamp on the sand. They were rather weakly positively phototropic, and after the light had been on the sand for some time, it could be noted that most of them were gradually orienting themselves toward it. They leap vigorously at the slightest motion near them. Like the storied Mormon cricket of the intermontane West (Anabrus simplex), these little beach crickets fell quickly upon an injured fellow and disposed of it with the rapidity and facility denoting the confirmed omnivore, which they were assumed to be, although no other data were obtained on their plant feeding habits, if any. Similarly, they were quite agile in catching the rather numerous small flying ants attracted to the light, and which were meandering about the sand. But, judging solely by their numbers, it is unlikely that predation was their usual way of making a living, for there didn't seem to be a large enough supply of available victims for the horde--

by contrast, the lush plant growth would seemingly have had to supply the bulk of the food such a population of crickets would require. Here, certainly, is one animal which can be reckoned an important factor in the conversion of plant materials and smaller animals into food available for other animals greater in size, and consequently occupying a more advanced spot in the food-cycle scheme. One of the larger animals patiently engaged in such conversion was the above-mentioned ghost crab; these were observed preying upon the small white cricket in large numbers. A rough count was made of the number of successful catches out of the number of attempts that any one ghost crab made, with the resulting approximation of 1 in 10.

An additional characteristic of Arno night beaches is the great number of crab spiders hunting on the rocks and vegetation bordering the sand. Directing a flashlight at eye-level usually struck up myriads of diamond-bright points of light--they could be seen flashing on all sides as the light swept along. Close inspection showed them to be the eyeshine of hunting spiders. Occasionally such a point of light turned out to be a small ground gecko, but with some experience, it soon became possible to distinguish these latter by virtue of their slightly larger size and more yellowish reflection.

Except for the beaches the shore is rocky, consisting of sharp, pitted elevated reefs. Here and in the strictly intertidal zone insects are virtually absent, contrary to the situation that exists in the Halophila tide pools of Samoa or the beaches of Hawaii. The one human element that enters into the picture in the intertidal zone is the presence of human feces--a hygienic habit involving use of the tidal waters for sewage disposal which attracts numerous flies that would otherwise be entirely absent from the

zone. Mangroves are a special association in a few places such as the lagoon at Bikariej. No insects were observed to inhabit the mangrove areas except marine water striders.

The Inner Beach is occupied by various plants such as Scaevola, which occurs singly or in pure stands and provides blossoms for the Marshallese head leis, Messerschmidia, Guettarda, Pipturus, Cordia, and, mostly on raised ledges, Pemphis. Each of these characteristic strand plants harbors a distinct fauna, a leaf mining agromyzid fly making conspicuous serpentine burrows in the thick Scaevola leaves, caterpillars of the Achaea moth on Cordia, the striking day-flying moth, Utetheisa, with red and black spots on a white background, on Messerschmidia and the beautiful blue Hypolimnas butterfly on Sida.

A particularly rich habitat in this zone is provided by the native custom of burning Scaevola and Messerschmidia thickets to provide space for coconuts. The dying or dead limbs with leaves browned but still attached, were attractive to two Scolytid beetles, one round-headed borer, and several small predaceous rove beetles. Also in the beetle galleries were two predaceous bugs of the family Anthocoridae and one curious little predator with the imposing scientific name, Ceratocombus.

The only seemingly barren tree in this association was Pemphis. Repeated search failed to reveal a single insect on this unusually hardwooded tree. Scaevola, on the other hand, supports a considerable population including a small endemic bug, Campylomma, each island group in the Pacific having a species with distinctive spots on its hind legs.

The Open Woodland. As one approaches Arno it is the erect trees that catch the eye. In profile, the tall trees give the island its place on the

horizon. Coconuts and the screw-pine (Pandanus) comprise most of the forest and are the exclusive elements that rise above the strand scrub in the narrow parts of Arno. The coconut-pandanus forest, whether seeded naturally or planted by man, is an open type with individual trees rather widely separated, allowing sunlight to reach the ground during most of the day.

Much has been written of the insect pests of the coconut in other parts of the tropics but Arno is singularly free from such troubles. The Micronesian coconut scale, an oval, reddish scale nearly one-fourth inch in diameter, is the most conspicuous pest on fronds and green husks. The boots, skirts and trunks, on the other hand, teem with insect life. Here one finds a whole community gathered largely for the protection afforded by this ubiquitous tree. Several kinds of cockroaches are found as well as small bark lice, earwigs, ants, etc. Most of these fall easy prey to the skinks which frequent the same habitat.

On Arno Pandanus is not so attractive to insects as the coconut, perhaps because it does not provide as good protection. Only at the bases of the fronds is a microhabitat found. Here rain water accumulates, sometimes in amounts sufficient to sustain dragonfly naiads and, in some parts of the tropics, mosquito larvae. On Arno during our stay moisture was sufficient only for earwigs and small beetles.

The fruit of the Pandanus is enormous and, when ripe, high in sugar content--this providing a delicacy for the natives. Decaying Pandanus fruits on the ground harbor an association of vinegar flies (Drosophila), fruit beetles (Nitidulidae) and numerous predators (Staphylinidae, Anthocoridae, Ceratocombidae). In addition there is a small but very active, white, predaceous mite.

The ground cover in the open woodland consists of various low plants such as Vigna marina, Wedelia, Fleurya and, in open areas, the sedge Fimbristylis, and associated grasses such as Lepturus. Sometimes this growth is choked by the parasitic vine, Cassytha. This ground cover is rich in insects, the undersides of Vigna leaves being heavily infested with the Micronesian red spider mite (Tetranychus), Vigna and Fleurya being spotted and withered by the hopping plant bug, Halticus, the grasses acting as hosts for the cosmopolitan green plant bug, Trigonotylus, and Fimbristylis harboring a remarkable community of true bugs including the herbivorous sedge bugs, Ninus and Orthotyllelus, and Nysius picipes, Pachybrachius nigriceps and Pachybrachius pacificus, and the predaceous Nabis capsiformis. That the lone predator is not sufficient to keep this association in check is attested by the enormous numbers of individuals present wherever the plants occur. The Nysius is of particular interest because it is found only on the islands remote from air bases in the Marshalls whereas Nysius pulchellus, from Guam, is found exclusively on Majuro and Kwajalein. Presumably Nysius picipes is an old resident in the Marshalls, yet it is indistinguishable from typical Wake Island specimens.

The Canopy Woodland. The richest zone on Arno occurs in the wider parts of the islets where humus has accumulated and breadfruit grows. Here one finds a dense growth of trees 50 and 75 feet tall with foliage so dense that the ground is shaded most of the time. Before the time of the present inhabitants, taro pits were dug in such places, thus further augmenting the accumulation of humus and the maintenance of moist conditions. Here one finds the buttressed trunks of breadfruit with epiphytic bird's-nest ferns, a moss, Calymperes tenerum, a thick, low undergrowth of Polypodium fern, and decaying logs with Polyporus and Schizophyllum fungi.

Here in decaying logs are wire worm larvae, stag beetle adults and larvae, termites, ants, Machilis and a large red Collembolan, wood roaches, earwigs, predaceous rove beetles, and other invertebrates such as scorpions, pseudoscorpions, centipedes, earthworms, isopods, and millipedes, as well as land snails of several species. On the fungi growing on the logs are fungus beetles (Ciidae and Endomychidae), fungus gnats (Mycetophilidae), and various predators that take advantage of such situations. Fallen logs are one of the most profitable foraging places for insectivorous skinks and birds.

Tree holes are frequent in this part of the forest and water stands in them for considerable periods. In this microhabitat the endemic Marshallese mosquito, Aedes marshallensis, breeds. The eggs are laid at the water's edge and the pale larvae feed on the very special type of organic matter at the bottom of such small bodies of water. That the mosquitoes thrive in spite of their rather restricted habitat is attested by the large numbers of individuals, yet these mosquitoes are of such retiring habits that they are seldom troublesome and only caused serious trouble during World War II when, on neighboring islands, dengue fever broke out. This mosquito, being an efficient vector, had to be controlled, but only in the vicinity of military installations because it has a short flight range.

Taro pits provide one of the most intriguing problems for the biologist. Surrounded by luxuriant tropical vegetation, these bodies of shallow water should, by all mainland standards, be teeming with life. Yet they are almost devoid of insects. A fresh water snail is always common but this is all that meets the eye at first glance. Mayflies, caddis flies, and all of the numerous water beetles and bugs are absent. Closer inspection reveals blood worms in the mud, from which a few midges emerge, the remainder

forming the basic, and in some instances the only, diet of the dragonfly naiades. These fierce predators with their extensible labia and powerful jet propulsion are quite the fiercest animals in the water and at least on Arno, are overadapted to their particular niche. The only other arthropod of any consequence in fresh waters is a reddish shrimp which was found occasionally.

The extremely depauperate fresh-water fauna is not surprising when one considers the nature of a coral atoll. Arno has a relatively heavy and uniform rainfall and therefore fares better than most atolls. Typically, fresh water is scant and seasonal on coral atolls and fresh-water life must be hazardous indeed. Even on Arno, the only endemic of aquatic habit is the tree-hole mosquito. The dragonflies are all strong-flying immigrants and the other forms may be accounted for by accidental transport of relatively recent date.

Adult dragonflies are swift fliers and are seen more in the open forest where they hover or dart about capturing gnats and other small insects on the wing. The slower and more fragile damselflies were seen only in the vicinity of the taro pits on the widest part of Arno Island. Damselfly naiades were not seen but dragonfly naiades were common in wells, cisterns and taro pits where they undoubtedly eke out a precarious existence in the face of occasional hurricanes and the ever-present danger of drought.

Herbivorous insects are not conspicuous in the canopy forests but nevertheless are abundant, a large red corizid bug occurring on Allophyllus and the bird's-nest fern (Asplenium nidus), a small but spry spider mite on breadfruit leaves and a host of small saprophytic and parasitic insects in fallen rotting breadfruit, as in the rotting Pandanus fruit. The productivity of one rotten breadfruit in terms of individual Drosophila flies is enormous.

Certain insects such as lice and bed bugs have accompanied man in all of his wanderings. The island peoples were no exception to this and it is certain that numerous species even less intimately associated with man than the above stowed away in native canoes. In this way, no doubt, the cosmopolitan house fly and its chief enemy, the predaceous Hermetia fly, came to Arno and also the Australasian and Oriental cockroaches, various ants, the rotten-fruit insects and the scale insects, mites and aphids which are attached to the coconut, breadfruit, Pandanus, banana, taro, arrowroot, papaya and lime trees. Also to be classed as a silent hitchhiker is the notorious dengue-yellow fever mosquito whose larvae have traveled over the entire tropical world in drinking water. On Arno, as elsewhere, this species is so closely associated with man that it is found only in and around houses and breeds in the cisterns and other drinking water containers, leaving the tree holes of the forest for the closely related Marshallese mosquito.

Termites attack man-made structures as well as native woods on Arno as elsewhere in the tropics. Four species, each belonging to a separate genus and each harboring distinctive Protozoa in its gut, were found on Arno. Without the Protozoa termites have been shown to be incapable of utilizing the dry cellulose of dead wood as nutritive material.

This is only a partial list of the camp followers of man in the Pacific. Nevertheless, it is a formidable array and causes one to wonder how it is that life is so pleasant on Arno. The fact is that none of these pests, except possibly the house fly, is sufficiently numerous to present a real problem in the daily life of the natives. In fact Arno is singularly free from such notorious scourges of the tropics as the coconut moth, the coconut

beetle, the Oriental fruit fly, locusts, etc. Even the ubiquitous copra beetle was not seen.

Agricultural Pests. At the time of our study there were no agricultural pests of any significance on Arno. This is a situation almost without parallel elsewhere in the world. The reasons for this happy state of affairs are complex. First, the number of crops is small and includes only those species best adapted to the conditions on a coral atoll. On Majuro, where beans and sweet potatoes are grown, hopping plant bugs (Halticus) and mealybugs are very numerous and destructive. Perhaps of greater importance, there is no intensive agriculture on Arno, the staple coconuts, Pandanus, breadfruit and taro growing with little or no cultivation and, except in the case of breadfruit, existing in amounts in excess of the actual needs of the population. The breadfruit being seasonal and especially favored as food, is more fully utilized, though no apparent attempt is made to plant new trees. Only bananas are planted in dense stands and these are protected, as young shoots, from pigs. Finally, the low level of insect pests must be attributed to the particular ecological relationship that exists on Arno between herbivores and predators. Normally, herbivores far outnumber predators in an animal community. On Arno, however, protected habitats are few and predaceous insects and vertebrates (mainly skinks) are exceedingly numerous (see Report by Marshall). Thus we have a situation in which the population level (equilibrium) of insects of agricultural crops is below the threshold of economic damage.

Ectoparasites. This subject was investigated by Dr. Marshall. A list of the parasites, both external and internal, of pigs, chickens, dogs and cats appear in his Report. Both the house rat and the Polynesian rat were

found on Arno and both were infested with lice (Hoplopleura) and two species of parasitic mites (Laelaps). Herons were infested with parasitic flies (Ornithoica) and mites, noddies with bird lice, Austromenopon, hippoboscid flies, and mites.

Insects in relation to health and sanitation. On Arno there are numerous insects and other invertebrates that affect the health of man either directly or indirectly. Scorpions and centipedes are much feared by the natives. Although we cannot say from experience, the bite of a centipede or the sting of a scorpion are usually of the same order of severity as a bad bee sting. Certainly scorpions and centipedes are sufficiently common so that their poisonous effects are experienced rather frequently. It seems safe to assume, however, that the natives' fears are exaggerated, on the basis of experiences elsewhere in the tropics.

The most serious arthropod bite in most parts of the world is that of the black widow spider. This spider has been reported from nearby islands in the Marshalls but we found none on Arno. Likewise we found no ticks, chiggers or fleas.

A rather unusual pest of man in the Marshalls is the so-called "Bao in jekaro" (BIRD IN THE JEKARO), a 3/4-inch, yellow oedomerid beetle with strong cantharitic poisoning properties. It came readily to night lights on Arno and was found on several occasions flying in cloudy weather. Everywhere we heard the same story: that it was strongly attracted to the "jekaro", the sap from the inflorescence of the coconut, while the latter was being tapped. If a "Bao" falls into the sap and is eaten or swallowed, it produces kidney disturbances, which are well-known aftermaths of cantharidin poisoning. If crushed on the skin, it would produce a blister--as we discovered from personal experience. Crushing an individual

experimentally on the forearm produced a wheal about the size of a quarter and a blister which broke after a couple of days.

The ectoparasites of man on Arno include lice and, presumably, the tropical bed bug, although bed bugs were found only on Majuro. The apparent absence of bed bugs on Arno is remarkable, since the natives say that they were found during the Japanese occupation. Whatever their true status may be they were certainly not conspicuous on Arno during the period of our study.

Lice, on the other hand, are rather common, especially head lice, and the natives engage in a louse-catching ceremony. There is no evidence of louse-borne typhus fever and this disease would not be expected in such a comparatively cleanly people in the tropics where excessively heavy, tight clothing is unknown.

Three mosquitoes are commonly encountered on oceanic islands in the Pacific, the common house or night-biting mosquito of the tropics, Culex quinquefasciatus, and the two day biters, Aedes aegypti and Aedes marshallensis. The first of these, although found on most islands of the Pacific, was not found by us on Arno, much to our surprise and pleasure, since it was not necessary to use our bed nets. However, night-biting mosquitoes have been reported by others. The pantropic dengue-yellow fever mosquito, Aedes aegypti, is common, but only in the immediate vicinity of human habitations. As is the case elsewhere in the world, this species, originally a tree-hole breeder in Africa has adapted itself to the human race even more intimately than most of our domesticated animals.

The eggs are laid at the water's edge in the concrete cisterns and other drinking water receptacles on Arno. The wary larvae are bottom feeders,

swinging with S-shaped movements from surface to bottom to provide for their constant need for air on the one hand and food on the other. Adults have silver-banded legs and lyre-shaped markings on the thorax. We found them commonly in houses, including our laboratory, where they lurked beneath tables and in dark corners biting surreptitiously around the wrists and ankles.

Dengue fever has been reported from the Marshalls, yellow fever has not. Neither disease is endemic so the only danger lies in the introduction of the virus in a human carrier, an unlikely event since the carrier would have to travel from the point where he was infected to Arno within the incubation period of the disease and be bitten by a local mosquito on or about the time of the onset of the disease. In spite of this intricate timing, dengue broke out on various islands in the Marshalls and Gilberts during World War II and the possibility of reintroduction should not be overlooked in establishing quarantine regulations.

The native Marshallese mosquito is also a day biter and a close relative of the dengue-yellow fever mosquito (they both belong to the same subgenus, Stegomyia). This is a tree-hole breeder, the larvae which look and act like aegypti larvae superficially, occurring in water-filled holes in breadfruit and other trees and in coconut half shells in the canopy forest of Arno. Adults swarm about when one stands still in the shade of a breadfruit tree but they are not vicious biters. This species belongs to the so-called "Pseudoscutellaris Group", pseudoscutellaris being a vector of non-periodic filariasis in Fiji and Samoa. We saw no evidence of filariasis on Arno (the chronic form known as elephantiasis is conspicuous in some parts of the Pacific).

Two groups of insects, the cockroaches and house flies, are of importance in general sanitation on Arno. The cockroaches, although exceedingly abundant, are less conspicuous because of their nocturnal habits. The night-feeding skinks and geckoes eat large numbers of these but the population is still sufficient so that a certain amount of contamination undoubtedly takes place.

Far more important hygienically, in fact the chief agent other than man himself in transmitting enteric disease organisms, is undoubtedly the house fly. This cosmopolitan pest occurs in enormous numbers on Arno. It is somewhat smaller and darker than mainland forms but is nonetheless abundant and bothersome. But for this pest Arno might well qualify as the "paradise" so frequently extolled in tourist posters. The combination of unscreened privies, defecation in exposed intertidal areas, unscreened houses and unprotected food, constitutes an "ideal" situation for the particular kind of contamination to which the house fly is adapted. There is little doubt that the incidence of amoebiasis as given in Marshall's Report is attributable in part, at least, to contamination of this type.

Aside from the obviously favorable breeding places, the large numbers of house flies may be attributable to the comparatively few natural enemies. Skinks cannot catch flies as readily as some other insects. There is an efficient larval predator, the larva of the large Hermetia fly. This largest fly on the island was found at all times in and about privies but unfortunately does not reduce the population of house flies effectively.

Interrelations of Insects with Plants and Animals of Arno

The "food cycle" (Elton) or "food web" (Allee, Emerson, Park, Park, Schmidt) becomes exceedingly complex, even for a small association. However,

an attempt has been made to show in the accompanying Tables (I-V) some of the food chains as they exist on Arno. Unfortunately, quantitative data on insect populations are not available so calculations of biomass are not possible. However, it may be accepted as a basic premise and this was confirmed in a general way by field observations, that the herbivores of small size were most numerous in individuals. The role of each species listed in the food chains is indicated by appropriate letters as follows: herbivores (H), predators (Pred), parasites (Par), Saprophytes (Sapr), and scavengers (Scav). In general, species are listed in order, starting with groups of herbivores, then proceeding to scavengers and then to successive groups of predators, members of each group preying on members of preceding groups. The departure from this scheme in Table V (The Human Community) is self-explanatory.

It is noteworthy that most of the food chains end with lizards. This is a partial explanation for Marshall's statement that lizards (the blue-tailed skink in particular) are the the most numerous land vertebrates on the atoll. This does not mean that the skinks have no enemies for they were eaten on occasion by cuckoos, herons, chickens and even by a land crab, Geograpsus. However, none of these predators is generally distributed and none depends primarily on lizards for food. Therefore the lizards are relatively free from predators. They do have numerous endoparasites, including stomach nematodes and rectal flagellates.

The significance of these data from the viewpoint of atoll ecology is that the majority of the food chains are independent of man. Only in the immediate vicinity of villages is the picture significantly altered and in such places man enters the basic atoll food chains mainly via chickens and pigs. Aside from this, man has moved into the atoll biota and made his own niche.

Origin, Dispersal, and Speciation

The origin of the fauna and flora of Arno is lost in antiquity but it is possible to piece together in a general way the probable history on the basis of present day observations and certain logical inferences.

First, if one of the presently accepted theories of formation of coral atolls is true (see Wells' Report), then the insects and all other animals and plants must have reached Arno fortuitously, that is, by accidental transport. Various types of overseas' dispersal are known to occur (see Zimmerman, Ins. of Hawaii), among which are wind and convection currents of the air, birds, rafts of debris carried by ocean currents, native canoes and, more recently, trading boats and airplanes. Probably all but the last of these have contributed to the present biota of Arno. While it is difficult definitely to attribute the presence of a particular species to a certain type of dispersal, here again we have certain facts and certain logical inferences to go on.

Certainly the insects associated with man, such as lice, cockroaches, and the house fly, came with man and probably with early man in native canoes. The dengue-yellow fever mosquito was probably a more recent immigrant, since its dispersal elsewhere in the Pacific (Hawaii, Usinger) is known to be associated with the voyages of exploration and profiteering during the 19th century.

Insects which are attached to breadfruit, coconut, Pandanus, arrowroot, banana, and lime (e.g., scale insects, aphids, etc.) surely came with these crops when they were introduced by the natives.

Many insects of small size have been collected at high elevations (a mite at 30,000 feet, for example) in a study of several years' duration

(Glick). Especially during the infrequent but violent hurricanes, small forms, whether winged or not, must have been blown to Arno. Stronger flying insects such as the dragonflies and the monarch butterfly, we know are capable of long distance flights, aided no doubt by the wind. Thus Anax has flown to ships at sea and readily establishes itself on remote islands, wherever fresh water is to be found. Similarly, the monarch butterfly, though absent when its milkweed host is wanting, arrives soon after the accidental or deliberate establishment of Asclepias curassavica.

Though rafts may be necessary to account for endemic skinks, many of the animals which present apparently insuperable problems of dispersal (e.g., land snails, wingless weevils, etc.) could have been transported on the feet of migratory birds (Zimmerman).

Beyond a certain point this type of reasoning degenerates into idle speculation amd is of little or no use to anyone. However, it is instructive to carry the analysis as far as possible in order to piece together the separate parts that contributed to the present biota of Arno. To a certain extent the same sequence of events can be traced when a new islet is built up from reef to sand bar and thence, through accumulation of vegetation, to a cemented and subsequently decomposed substrate capable of supporting life as we find it on the densely covered islets. Literally all stages in this succession can be seen today. But this is not the end. Acultural processes are proceeding at an accelerated rate on Arno as elsewhere in the world (see Mason's Report) and the biota is bound to change too. In the long run this may be regarded as inevitable and therefore of no particular concern. However, the depauperate nature of the biota (e.g., the small number of different kinds of plants and animals as compared with an equivalent mainland area) and of even greater importance, the disharmonic

nature of the biota (e.g., the complete absence of certain types with consequent gaps or ecologic vacua) makes Arno peculiarly susceptible to disruptive influences. Furthermore, the limited economy of the people, based as it is on so few crops, could be brought to a standstill by failure of one of the staples. Hence, it is important to look to the future and try to foresee immediate and long-term dangers which might ensue from the dispersal and establishment of noxious plants and animals from nearby or farther distant islands and mainland areas.

The most imminent cases of this kind are on the neighboring atoll of Majuro. Due to wartime activity and air transport, Majuro, and to an even greater extent, Kwajalein and Eniwetok, now support several immigrant insects which, if introduced to Arno via the native canoes or the copra boat, would prove to be detrimental to the natives. Foremost among these potential immigrants are the infamous migratory locust and a second, slightly smaller grasshopper, the black widow spider, the night mosquito, an Odynerus wasp and a tick. In addition, bed bugs, fleas, the coconut Brontispa beetle and the copra beetle are either absent from Arno or are so scarce that we did not find them. Obviously an effort should be made to prevent or delay their establishment or increase on Arno.

Serious pests from more distant islands of Micronesia include the giant African snail, the Rhinoceros beetle (Oryctes), and a malaria mosquito, any of which could reach the Marshalls from Guam or Saipan unless quarantine regulations are strictly enforced.

Table I

Strand Community

A. Open Beach Stratum - Mostly Nocturnal

Sand crickets - H.
Sand fleas - S.
House flies - (human feces). Sapr. (daylight).
Robber flies - Pred. (Daylight).
Marine water striders (blown onto beach) - Pred.
Crab spiders - Pred.
Ghost crabs - Pred.

Rock geckoes - Pred.

Plover - Pred.
Curlew - Pred.
Tattler - Pred.

Marine Insect "Community"

A. Surface Stratum

Pelagic plankters - Pred. H.
Marine water striders (Large - Open ocean) (Large - Tidepool species) (Small - Protected coves) Pred.

Table II

Inner Beach Community

A. Foliage Stratum

Leaf-mining fly - H. Scaevola
Plant bugs - H. Scaevola
Caterpillars - H. Cordia, Messerschmidia, Sida
Leaf-cutting bee - H.
Aphis - H.

Ants - Scav.

Ladybird beetles - Pred.
Green lacewings - Pred.
Syrphid flies - Pred.
Spiders - Pred.

Geckoes - Pred.
Skinks - Pred.

B. Bark and Dead Wood Stratum

Bark beetles - Wood borers
Round-headed borers - Wood borers

Rove beetles - Pred.
Predaceous bugs - Pred.
Spiders - Pred.

Geckoes - Pred.
Skinks - Pred.

C. Ground Stratum

Sand crickets - H.

Crab spiders - Pred.
Ghost crabs - Pred.

Rock geckoes - Pred.

Golden plover - Pred.
Heron - Pred.

Table III

Open Woodland Community

A. Coconut - Pandanus Stratum

Coconut scale - H.
Sugar-cane weevil - H.
Bark lice - Scav.
Ants - Scav.
Cockroaches - Scav.

Earwigs - Pred.
Luteva - Pred.
Spiders - Pred.

Geckoes - Pred. Night
Skinks - Pred. Day and Night

B. Ground Cover - Vigna, Wedelia, Fleurya, Fimbristylis, Lepturus, Cassytha

Red spider mite - H. Vigna leaves
Hopping plant bug - H. Vigna and Fleurya
Green grass bug - H. Grasses
Leafhoppers - H.
Sedge bugs - H. Fimbristylis
False chinch bugs - H. Fimbristylis
Thrips - H.

Bees - H.
Caterpillars - H.
Mealybugs - H.
Aphids - H.
Ants - Scav.

Damsel bugs, Nabis - Pred.
Spiders - Pred.
Thrips - Pred.
Stink bugs - Pred.
Ladybird beetles - Pred.
Green katydids - Pred.

Geckoes - Pred. Night
Skinks - Pred. Day and Night

Table III (continued)

C. Fallen Green Coconuts

Rats - H.
Coconut crabs - H.
Mosquitoes - Larvae-detritus.

D. Rotten Pandanus Fruit Stratum

Vinegar flies - Sapr.
Fruit beetles - Sapr.

Rove beetles - Pred.
Spiders - Pred.
Predaceous bugs - Pred.
Predaceous mites - Pred.

Geckoes - Pred.
Skinks - Pred.

E. Soil Stratum

Earthworms - Sapr.
Millipedes - Sapr.
Sowbugs - Sapr.
Garden centipedes - Sapr. H.
Silverfish - Scav.
Ants - Scav.

Hermit crabs - Pred. Scav.

Rock Geckoes - Pred. Night
Ground skinks - Pred.

Table IV

Canopy Woodland Community

A. Breadfruit Stratum

Corizid bug - H. Bird's nest fern
Leafhoppers - H.
Spider mite - H. Breadfruit leaves

Mosquito larvae - Detritus. Tree holes

Ants - Scav.

Spiders - Pred.

Geckoes - Pred. Night
Skinks - Pred. Day and Night

B. Underbrush Stratum - Alophyllus, Pipturus, Terminalia, Pisonia, Cordia

Aphids - H.
Mealybugs - H.
Leafhoppers - H.
Corizid bugs - H.
Fruit flies - H.

Ants - Scav.

Spiders - Pred.
Ladybird beetles - Pred.
Syrphid flies - Pred.

Geckoes - Pred. Night
Skinks - Pred. Day and Night

C. Fallen Log Stratum

Fungous flies - Sapr.
Fungous beetles - Sapr.

Weevils - Woodborers
Termites - Wood feeders

Wireworms - Sapr.
False wireworms - Sapr.
Stag beetles - Sapr.

Ants - Scav.

Table IV (continued)

C. (cont.)

Earwigs - Pred.
Spiders - Pred.
Pseudoscorpions - Pred.
Scorpions - Pred.

D. Rotten Breadfruit Stratum

Vinegar flies - Sapr.
Fruit beetles - Sapr.

Rove beetles - Pred.
Spiders - Pred.
Predaceous bugs - Pred.
Predaceous mites - Pred.

Geckoes - Pred.
Skinks - Pred.

E. Soil Stratum

Earthworms - Sapr.
Millipedes - Sapr.
Sowbugs - Sapr.
Garden centipedes - Sapr. H.
Silverfish - Scav.
Springtails - Sapr.
Ants - Scav.

Rock geckoes - Pred.
Ground skinks - Pred.

F. Taro Pit Aquatic Stratum

Midge larvae - Detritus
Shrimp - Pred.
Snails - H.
Dragonfly naiades - Pred.

Table V

Human Community

Man - Omnivorous. Eats fish, coconut, breadfruit, taro, pandanus, bananas, papaya, and various imported foods.

Ectoparasites - Lice, bedbugs
Endoparasites - Amoebae, hookworms, etc.

Domesticated Animals

Dogs - scavenger - copra - garbage
Pigs - scavenger - soil insects, roots
Chickens - Omnivorous. Copra, ground insects, skinks
Cats - Omnivorous. rats

Household Vermin

Rats - Eaten by cats

Ectoparasites - mites and lice

Cockroaches - Evania parasites
Termites
Mosquitoes - cisterns - Dragonfly naiad predators
Houseflies - Hermetia parasites - Privies
House gecko eats all household insects

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The Land Vegetation of Arno Atoll, Marshall Islands

by

William H. Hatheway

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William H. Hatheway
Harvard University
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INTRODUCTION

In 1952 78 percent of the land surface of Arno atoll was under coconut and breadfruit forests, both of which types were maintained as such only by periodic clearing of unwanted wild plants. With the exception of recently introduced weeds, virtually every species of plant on Arno found a specific use -- in medicine, construction of houses, canoes, and implements, or in the weaving and coloring of mats, to mention only a few. The possibility that even wild native species had been planted on some sites they occupied could never be overlooked. Obviously, Arno's vegetation was inseparably linked with its people. To the student who regards vegetation as simply the result of the interaction of flora and habitat, inhabited atolls such as Arno can be extremely confusing. On the other hand, a study of the interrelations of the people and the plants of an atoll is interesting not only in the insight into the life of the atoll people which it provides, but also in its illumination of certain important processes of vegetational and edaphic change which might otherwise not be understood.

About 1000 persons were resident at Arno in 1952, most of whom lived in villages along the lagoon shores of the wider islands. Islands less than 600 feet wide and stony lands were for the most part uninhabited. Dwellings were concentrated near the lagoon shores of the wider islands, for these sites, besides providing easy access to the lagoon, were conveniently near those areas best suited for certain food plants -- the breadfruit and the yaraj (Cyrtosperma). In the interiors of the wider islands the salinity of the ground water was sufficiently low to permit their growth. The villages, however, were not always conveniently near

coconut groves. Copra-making parties often had to travel considerable distances to their work.

At Arno right to the use of the land was held not by individuals but instead by extended family groups (bwij), the heads of which were termed alabs. The land holding (wāto) was commonly a narrow strip of ground one to five acres in area extending from lagoon to ocean. In many cases a bwij held rights on more than one wāto. From its wātos the bwij harvested much of its food and wood and all of its copra. The latter produce constituted the chief source of cash income to the bwij, from which its members purchased imported foods, clothing, soap, kerosene, and other trade goods. Land could not be bought or sold; the right to the use of the land was passed in strict hereditary fashion from one generation of the bwij to the next. Aside from a very small area claimed by the United States Government, there was no public land on Arno. Right to the use of each piece of land on the atoll was claimed by at least one bwij. Consequently, it is obvious that the vegetation found on any piece of land was dependent upon the previous use of that land by its bwij.

Intensity of land use depended not only on the suitability of the land holding for the growth of economic plants, but also on such factors as its distance from the places of residence of the bwij, the number of acres per bwij member, and very probably on the industriousness of the members of the bwij, especially the alab. My assistant informed me that the bwij of which his father was alab, was unable properly to take care of all the land which historically it had been alotted. "Some have too much land. Some don't have enough." At Majuro atoll brush had grown up on land occupied by the United States Government during the war and

since abandoned. The former Marshallese "owners" had by no means relinquished claims to this land, but were not certain of their legal rights to its use. Land disputes were all too common at Arno. Since the author was advised not to become involved in such disputes he did not investigate their relationships to the intensity of use of the land.

In 1952 the flora of Arno atoll consisted of about 125 species of vascular plants (cf Anderson, 1951). Of these nearly half had been introduced within the past 100 years, roughly 38 intentionally as cultivated plants and 19 accidentally as weeds. That is to say, the Arno flora of 1850 consisted of approximately 68 species of higher plants. Of these, however, probably about 24 had been introduced by the Marshallese as economic plants or weeds. Although a native flora of approximately 44 species may seem very small, that of Arno is relatively rich compared to the floras of other low islands situated at greater distances from the rich source of seeds of Malaysia and Melanesia, or receiving less rainfall. Canton Island in the Phoenix group, relatively near the rich flora of Fiji, has a native flora of only 16 species, but it is nearly a desert. Palmyra Island, lying to the east of Arno, receives about as much rainfall as the latter atoll, but it is much more remote from major sources of seed. Its flora consists of only 16 species.

Although the flora of Arno is larger than that of many atolls, it is small and relatively uninteresting compared to the rich floras of high islands like Fiji, Hawaii, Tahiti, or even Ponape. Not a single vascular plant species is restricted to Arno atoll. All of the native wild species are wide-ranging plants, most occurring on the shores of islands in both the Pacific and Indian Oceans, and at least 7 -- 16 percent of the native flora -- occur naturally in the tropics of both hemispheres. Except for a

single species, Pisonia grandis, all of the native plants of Arno possess seeds or fruits which are distributed by wind or ocean currents. The fruits of the Pisonia are glutinous and adhere to the feathers of the wide-ranging seabirds which roost and nest in its branches. It is not surprising, then, that this tree occurs on nearly every high and low island in the Pacific and Indian Oceans which is sufficiently moist to permit its growth, as do, indeed, a large proportion of the other native species of the Arno flora.

The climate of Arno is probably not very different from that of nearby Majuro, where annual rainfall is of the order of 120 inches. The winter is marked by stronger, more constant northeast trades and by somewhat less rain than the summer. Mean annual temperature is 81° F.; mean monthly temperatures vary only within 2° of the yearly average. The diurnal variation is about 10°; nights are pleasantly cool.

Arno atoll contained 133 islands and islets in 1952, which formed 5 square miles (3200 acres) of dry land. Almost all these islands had the same structure. Their seaward sides consisted of ridges of boulders, cobbles, and stones thrown up on the reef flats by storm waves. Sand accumulated on the lagoon sides of these boulder ridges, and dunes formed where a sandy beach faced the prevailing northeast trades. Between the stony ridge of the ocean side and the dune ridge of the lagoon shores, was often an interior depression. The islands tended to increase in width by additions of sand on the lagoon side, and coarser material on the ocean shores.

The ground water of an atoll islet is characterized by the presence of a Ghyben-Herzberg lens of fresh water. The depth of this lens and its salinity depend on the distance to the beaches and the permeability of the soils. Stony land is much more permeable to the salt water of the ocean

than is dune sand, and with the rise and fall of the tides appreciable mixing of fresh and salt water occurs. Thus the stony land of the ocean side of islands is underlain by much more saline ground water than lagoon-shore dunes. The ground water in the interiors of the wider islands is remarkably free from salt. Cox (1951) found only 8 ppm chlorides in a well at Ine about 500 feet from the lagoon; in an interior pool on Tatu Island only 200 feet from the ocean I found only 15 ppm. 150 feet from this pool the ground water in the boulder rampart had a chloride concentration of 7100 ppm, about 470 times as great. Fosberg (1949) and Cox remarked that ground-water salinity apparently acts as an effective control on the distribution of the breadfruit, an economic plant of aboriginal introduction. Variations in salinity affect the distributions of species of the wild native flora as well; the tolerance to salt of species of the Rhizophoraceae (mangroves), Pemphis acidula, and others is, of course, well known.

As Stone (1950) and Wells (1951) pointed out, typhoons occur about 4 times per century at Arno, and have left their mark on the islands in many ways. The washing away of entire islets is a spectacular consequence of typhoons, but windthrow and partial inundation have affected soil and vegetation. In certain local areas on Kilange Island, for example, nearly every large breadfruit tree was blown down in the typhoon of 1918 and large quantities of soil were thus disturbed. In other places considerable amounts of sand and rock had been suddenly dumped on low land, or the surface layers had been washed out. Such areas were often characterized by low organic and nutrient content of the surface horizons. The more superstitious believed such land to be inhabited by malignant spirits which hinder the growth of plants. Stories of hallucinations caused by these demons were common.

Relatively minor changes were constantly occurring along beaches. Between Ine and Matolen, for example, the shoreline was eroding in places, and plants which formerly grew along low dune ridges were stranded on the beach. A Pemphis tree with several pebbles embedded in its wood 3.2 feet above the present level of the ground was discovered growing on a sandy beach 15 feet from an eroding dune containing similar pebbles near its surface. The tree had in effect moved 15 feet toward the lagoon during its lifetime. Near Lukwōj coconut trees, which had previously toppled onto the beach as the dune upon which they were growing was undercut, were being covered with sand as the beach again built up. Entire trunks were buried save for the erect terminal parts, about 5 feet tall. The leaves were nearly twice as long, and some trees were bearing heavily.

The vegetation of Arno atoll is here classified into 9 types (Table I). These are merely arbitrary groupings of aggregates of plants into units convenient for description, analysis, and mapping. This, however, is not to deny that interrelations may be found between plants growing near one another. The vegetational map has been drawn from 1944-1945 aerial photographs taken by the United States Navy, supplemented by ground observations and interpretation of oblique photographs taken by the Navy in 1952. In general, the vegetational types listed in Table I are only those which could be distinguished clearly on the aerial photographs. Thus "scrub forest" is mapped as a single unit, but is divided into 4 subtypes in the descriptive text. Boundaries between the types are, of course, no less arbitrary than the types themselves. Even on the ground it is not always possible to classify with certainty as "coconut type" or "scrub forest" a stand of small, wild native trees through which coconut trees projected. Breadfruit groves were usually characterized by a rank undergrowth of native

trees and vines. "Secondary forest", on Arno island contiguous with extensive "breadfruit groves", usually contained numerous breadfruit trees. Obviously a line separating "secondary forest" from "breadfruit grove" must be based to some degree on a subjective estimate of intensity of use, illustrating the fact that on Arno vegetational study was inseparable from cultural anthropology.

TABLE I

Type	Number of Stands	Acres	Average size of stand (acres)	Percent
Coconut	147	2224.0	15.3	69.38
Productive	137	2127.4	15.5	66.37
Laora	1	65.5	65.5	2.04
Mellal	9	31.0	3.4	0.97
Breadfruit	53	277.0	5.2	8.64
Scrub Forest	143	566.3	4.0	17.67
Saline Flat	5	29.6	5.9	0.92
Mangrove Swamp	13	26.8	2.1	0.84
Fresh-water Swamp	3	6.6	2.2	0.21
Secondary Forest	8	74.9	9.4	2.34
Total	372	3205.3	8.6	100.00

COCONUT TYPE

Primary species: Cocos nucifera

Height of trees: 40 to 50 feet, exceptionally to 80 feet

Density: about 95 trees per acre, exceptionally as low as 40 or as high as 140 trees per acre.

69 percent of the land area of Arno atoll was under coconut forest in 1952, for copra formed the main article of export of the atoll. Copra production was feasible on practically the entire land surface of the atoll, saline flats and swamps and certain parts of the interiors of wider islands forming the only significant exceptions to this rule. The wide interiors of islands, however, were devoted in large measure to food production for local consumption, and the exceptionally rich phosphatic soils of Takleb and Namwi had been given over to some degree to such special crops as Kapok, Papaya, and Banana. Remote, narrow, or stony lands, areas in which the ownership of the land was in dispute, or lands the workers of which were less energetic than others, in some cases supported stands of wild native trees.

The coconut thrived over an extremely wide range of environmental conditions. It was productive over a 1,000-fold range of ground-water salinity and over at least a 50-fold range of concentration of available phosphorus. It was found on all habitats from fresh-water swamps to dry, windswept dunes, on organic mucks, fine or coarse-textured sands, or among fragments of coral rock. Except on those few areas in which it was not productive, the coconut was utterly worthless as an indicator of environmental differences.

The plants which grew under the coconuts, however, were not always the same in the different habitats on which the coconut was planted. Consequently, it is convenient to recognize three environmental subtypes within the coconut type, corresponding to the 3 major physiographic divisions of an atoll islet.

1. Lagoon shores and dunes

Secondary species: Pemphis acidula, Scaevola frutescens,

Hernandia sonora, Calophyllum inophyllum, Barringtonia asiatica, Suriana maritima, Pandanus tectorius, Sophora tomentosa, Canavalia microcarpa, Ipomoea tuba

Ground layer: Lepturus repens, Fimbristylis atollensis, Thuarea involuta, Cassytha filiformis, Triumfetta procumbens, Vigna marina, Tacca leontopetaloides, Polypodium scolopendria, Euphorbia chamissonis, Canavalia sericea

The coconut trees usually overhung the lagoon, sometimes toppling onto the lagoon beach where the shoreline was eroding. Along the lagoon shores of the leeward islands Pemphis acidula, a much-branched low tree with exceedingly heavy, hard wood, was often abundant on exposed beach-rock. In or near villages Hernandia sonora and Calophyllum inophyllum were observed, the latter commonly being used for rain catchment. On dunes Lepturus, Fimbristylis, and Thuarea formed a low, dense cover under the coconut trees.

2. Low Interiors

Secondary species: Morinda citrifolia, Pandanus tectorius, and other trees of the scrub forest type.

Ground layer: Lepturus repens, Fimbristylis atollensis, Thuarea involuta, Wedelia biflora, Cassytha filiformis, Triumfetta procumbens, Vigna marina, Polypodium scolopandria, Euphorbia heterophylla, Tacca leontopetaloides, Asplenium nidus, Nephrolepis sp. Boerhavia diffusa.

Fimbristylis and the grasses grew taller here, and Pandanus, sprouts of Morinda, Guettarda, and other trees of the scrub forest formed jungles in some poorly tended groves. Epiphytic mosses, Nephrolepis, and Asplenium appeared on stumps, fallen logs, and rocks. The velocity of the wind was much reduced and the habitat seemed moister.

Boulder ridges and stony land

Secondary species: Trees of the scrub forest type

Ground layer: Asplenium nidus, Nephrolepis sp., Wedelia biflora, Polypodium phymatodes, Fimbristylis atollensis, Lepturus repens, Triumfetta procumbens, Vigna marina, Thuarea involuta.

Ground cover tended to be spotty among the rock fragments of boulder ridges; less than 5 percent of the ground might be covered with vegetation. The ferns Asplenium, Nephrolepis, and Polypodium, together with patches of Wedelia in openings, were perhaps the most abundant plants. Invasion by wild trees from stands of native forest along the ocean necessitated nearly constant clearing, and in many places thickets had grown up to such an extent that collection of fallen coconuts was impracticable.

Types of Poor Coconuts

About 4 percent of the acreage under coconuts on Arno Atoll was relatively unproductive. The Marshallese recognized two types of "poor coconuts:" "Laora" and "Mellal." Each had a fairly consistent set of characteristics which, with practice, could be recognized easily.

1. "Laora" on Arno atoll occurred on Arno island and in the breadfruit belt in Ine village. In its extreme form on Arno island "Laora" was charaterized by:

Yellowing and scorching of the leaflets of the coconuts, most severely at the tips. Areas adjacent to the midribs were usually green.

The leaflets were sometimes twisted and more or less knotted together.

Dead leaves tended to hang on the tree.

The trunks of the coconut trees were sometimes blackened.

Density of stocking was low -- about 40 trees per acre in the worst affected areas of Arno island.

Dead trees were conspicuous. About 35 trees per acre were dead in the worst affected areas of Arno.

The older trees were mostly barren of fruit, although they produced

inflorescences. Apparently the fruits aborted at an early stage of development.

The younger trees bore fairly well; their water was exceptionally sweet.

In the worst affected areas of Arno island the ground cover consisted of clumps of Fimbristylis atollensis, covering the ground between which was a leathery black blue-green alga resembling a crustose lichen. Tacca leontopetaloides was common. Its leaves were yellow except along the veins and were characterized by the presence of circular brown spots 1/8 to 1/4 inch in diameter.

Laora was restricted to the interiors of the wider islands, where it occurred on soils of the Arno series.

The Arno people attributed "laora" to a "lack of salt." It is true that areas on which the malady was present contained very little sodium chloride in the ground water. Productive coconuts, however, occurred on sandy soils no less distant from lagoon and ocean and thus probably containing no more available sodium. It will be noticed (Fig. 13) that the area of poor coconuts on Arno formed a semi-circle around an area of secondary forest containing numerous abandoned house-sites and yaraj (Cyrtosperma) pits. On small clearings within the secondary forest the coconuts invariably exhibited severe "laora" symptoms. As one proceeded radially from the former center of habitation immediately on the lagoon side of the yaraj pits, the malady appeared to become progressively less severe. It is thus possible that the poor growth of coconuts in part of the interior of Arno island was related to the former use of the land for human habitation.

2. "Mellal", unlike "laora," occurred at or near the shores of islands. Its distinguishing features were:

General yellowing of the leaves of the coconuts. New leaves were slow to turn green.

The palms appeared stunted and probably died early (trees in laora areas were often very tall).

Dead leaves did not fall readily.

The trees bore only a few nuts.

Ground cover was invariably depauperate, consisting chiefly of an open stand of bunchy Lepturus repens.

The parasitic vine, Cassytha filiformis, was usually abundant.

Intsia bijuga grew as a straggling shrub, although on better sites it became a tree 60 or more feet tall.

Polypodium scolopendria was often common.

Mellal occurred at or near the lagoon or ocean shores of islands, on immature soils of the Shioya series.

Stone suggested that the poor growth of these coconuts might be attributed to sodium toxicity. Analysis by the present author of the ground water in an area of "mellal" on Langar island demonstrated only 135 ppm. chlorides. Judging from the relatively slight accumulation of organic matter in their upper layers, the "mellal" soils appear to be young, and may have resulted from washouts or heavy deposition of sand during typhoons. It is here suggested that many mellal soils may be deficient in nitrates, but that these deficiencies probably do not become striking until more than 30 years after the original deposition of a soil or the exposure of a fresh surface in a typhoon. Areas washed out during the

1918 typhoon supported apparently vigorous stands of young coconut trees. A legend stated that the "mellal" area of Langar island was buried under sand deposited during an ancient typhoon. In excavating a pit to the water table, however, the writer encountered no buried profiles.

Economics of Copra Production on Arno

The price of copra has fluctuated widely since 1950. Mr. H. E. Blodgett, manager of the Island Trading Company, Majuro, paid the following prices per ton of copra delivered (on ITC trucks) at Majuro:

Jan. 1, 1950	$100
Jan. 1, 1951	110
Feb. 10, 1951	130
June 16, 1951	115
Oct. 1, 1951	105
Jan. 1, 1952	95
April 1, 1952	70
July 1, 1952	70
Sept. 1, 1952	70

The 1952 price of 3½¢ per pound, after fixed costs were deducted, left very little for the "ri jerbal" (workers). The chief costs were:

Share of the iroij	1¢
Share of the alab	0.4
Shipping costs (Arno-Majuro)	0.7
Total	2.1¢

That is, at the price of 3½¢ per pound, the ri jerbal netted only 1.4¢ per pound ($28.00 per ton). The share of the iroij was fixed; it did not fluctuate with the price paid by ITC Majuro. I believe the same was true of the share of the alab.

At the rate of 1¢ per pound of the 622 tons of copra sold at Majuro, income of the iroij of Arno in 1951 was about $12,400, or $5.54 per acre of coconut land. Although the political and social prestige of the royal classes of the Marshall Islands is said to have declined (Spoehr, 1949), their economic position has probably improved with the introduction of the copra trade.* The relatively large income derived from "rent" of copra land may have been a primary consideration in the revolt of the three iroij erik of Liwaito (Mason, 1952). In 1952 these men in effect considered themselves iroij lablab on at least part of their land -- that is, they demanded (but did not always receive) the share of the iroij on that land.

In 1951 ITC Majuro purchased 622 tons of copra from Arno atoll. This copra was produced by about 216,000 trees

TABLE II

Type	Estimated coconut trees per acre	Acres	Total Trees
Coconut	95	2127	202,000
Laora	60	65	3,900
Mellal	70	31	2,200
Breadfruit	15	277	4,150
Scrub Forest	5	566	2,830
Pandanus swamp	45	6	270
Secondary forest	10	75	750
Total			216,100

* A considerable proportion of the copra share of the iroij was set aside by the council of alabs for the payment of extraordinary medical expenses incurred by Arno residents. The prestige of the iroij, however, was probably not lessened by such philanthropies, however involuntary they may have been.

In shipping copra the dried coconut meat was stuffed into coffee bags. The contents of about 350 nuts were sufficient to fill one bag, which then averaged about 106 pounds in weight. That is, the contents of a single nut, when dried, weighed about 0.303 pound on the average. It follows that the contents of 4.11×10^6 nuts produced on 2.16×10^5 trees were exported to Majuro in 1951. Thus, the average number of ripe nuts harvested for copra was 19.0; 0.28 tons were produced per acre of coconut land.

Local consumption of coconuts as food is here estimated from the Majuro data of Spoehr (1949; p.153). In 1947 58 persons belonging to 7 households consumed in 21 days 1083 nuts and 607 quarts of coconut toddy (jukaru). It is difficult accurately to estimate the equivalent of the toddy in nuts. Copeland (1931) stated that 5785 coconut trees in the Philippine Islands produced an average of 0.65 liter per tree per day in the year 1909-1910. In making jukaru an inflorescence of the coconut tree is cut off and the sap dripping from the cut stalk is collected over a period of 2 to 3 weeks. Assuming, conservatively, that the inflorescence would have produced 5 nuts had it not been cut, one quart of jukaru is approximately equivalent to 0.45 nut. Thus the total consumption of coconut products as food reported by Spoehr was approximately the equivalent of 1355 nuts, or 1.1 coconut per person per day. I suspect this figure is conservative if applied to Arno. Majuro village was crowded with war refugees in 1947, when Spoehr made his study, and coconuts were probably in short supply. Accepting this figure as being of the correct order of magnitude, however, the total local yearly consumption of coconuts as food at Arno is about 400,000

nuts, or about 1.85 nuts per bearing tree. Nuts processed locally for coconut hair oil and massage would probably bring the figure to 2 nuts per bearing tree. This total is the equivalent of about 60 tons of copra.

Summarizing these data for local and export production, on Arno atoll about 21 nuts were harvested per bearing tree in 1951, the equivalent of a production of 0.31 tons of copra per acre of coconut land. How do these figures compare with those of other copra-producing areas? Webster (1920: p.43) stated that "owing to close spacing and no cultivation, the average annual yield per tree in the Philippines is estimated at 25 nuts," but that on well managed plantations an average of 60 nuts per tree could be expected. Cooke (1932) reported that in well managed plantations in Ceylon on good sites where the number of trees per acre was 48 to 60, yields of 66 to 86 nuts per tree were obtained and that 15 piculs (0.9 tons) of copra per acre were harvested. Child (1950) estimated* that world production of copra in 1938 was 3,906,143 metric tons, produced on about 9,616,000 acres, or about 0.45 tons per acre (a metric ton equals 2204.6 pounds). The estimated production in the "Pacific Territories" was 0.333 tons per acre.

It is apparent that Arno's per-tree and per-acre productivity is low compared with that of the world, and even with that of the average of the "Pacific Territories." This low productivity is probably in part due to inefficient harvesting, although probably no more than 25 nuts per tree could be expected, given the crowded conditions of the existing groves. Total production of the atoll could no doubt be increased by converting some of the land under scrub forest to coconut

* "Based on Schnurmacher's Review of Coconut Products for 1938, Manila, 1939. Table IV, p.22."

plantations. Much of this land, however, is not well suited to copra production, as most of it consists of boulder ramparts and stony land exposed to wind and salt spray. Assuming that all this land be planted to coconuts, the acreage under coconut plantations would be increased only 25 percent over that of 1952. The gains in copra production to be obtained by increase in acreage or more efficient harvesting are probably slight, however, compared to those which might result from more careful management than was practiced in 1952. If the groves were thinned, competing vegetation kept more efficiently in check, the practice of applying phosphate and perhaps potassium fertilizers initiated, and a program of introduction of high-producing races established, per-acre productivity might well be doubled. The introduction of a variety such as the Philippine Romano would save considerable labor in making copra. Only 3,270 Romano nuts are required to make one metric ton of copra on Mindanao (Webster, 1920), whereas about 7,280 nuts were necessary at Arno in 1952.

It is obvious, however, that programs designed to increase copra production at Arno and elsewhere in the southern Marshalls would require changes in social patterns which might be undesirable or unpopular. Although complaints about the low price of copra and the resulting low income of the "ri jerbal" were frequent in 1952, it was the author's impression that the people of Arno were not eager to acquire wealth and property. Regular working hours were unknown. To produce enough copra to buy cigarettes, needles, thread, soap, fishing line, hooks, and other trade goods to last his immediate family one year, a man had only to work two to three weeks at making copra. Much time was spent fishing, visiting, and talking. More efficient management of the Arno coconut

groves would possibly double the cash income of the "ri jerbal", but only at the sacrifice of leisure hours. Abundant leisure time is perhaps one of the most pleasant aspects of Marshallese life. Programs that might decrease it in the name of increased efficiency should be recommended only after careful consideration has been given to their sociological implications

BREADFRUIT TYPE

Primary species: Artocarpus altilis (15 to 30 trees per acre)

Secondary species: Cocos nucifera (10 to 15 trees per acre)
Pandanus tectorius
Premna obtusifolia
Allophylus timorensis
Pipturus argenteus
Guettarda speciosa
Morinda citrifolia

Ground layer: Wedelia biflora
Tacca leontopetaloides
Lepturus repens
Thuarea involuta
Fleurya ruderalis
Fimbristylis atollensis
Polypodium scolopendria
Asplenium nidus
Nephrolepis sp.
Vigna marina
Centella asiatica
Ipomoea tuba
I. littoralis
Oplismenus sp.
Triumfetta procumbens
Hedyotis biflora
Alocasia macrorrhiza
Crinum asiaticum
Stenotaphrum subulatum

Yaraj pits: Cyrtosperma chamissonis
Musa paradisiaca
Hibiscus tiliaceus
Colocasia esculenta
Clerodendrum inerme

A considerable proprotion of the centers of the wider islands was occupied by breadfruit forests. A common approximate boundary of this type on the lagoon sides of islands was the main village path parallel to the lagoon. On relatively narrow islands the boundary on the ocean sides was often the beginning of the stony land complex or boulder ridge. On wider islands, however, the breadfruit zone usually did not extend

this far, for potential breadfruit land not needed for food production was given over, where feasible, to copra culture.

The breadfruit type was best developed at Ine, where pigs had not been allowed to run wild and devastate the yaraj (Cyrtosperma) pits, as they had at Arno, Bikarej, and Tutu. At Ine these pits were about 15 to 20 feet wide, 30 to 80 feet long, and 5 to 10 feet deep; earth heaped up around their sides formed the soil upon which the breadfruit and plants associated with it grew. The breadfruits grew as widely scattered trees 50 to 70 feet tall, with spreading crowns 25 to 75 feet in diameter. A striking feature of this type was the nearly complete absence of small diameter classes. Breadfruit trees between one and eight inches in diameter were definitely uncommon; most were 18 to 36 inches in diameter above the buttresses. Coconuts were common in the forest, but occupied only a small proportion of the canopy. Sprouts of Allophylus, Premna, Guettarda, and Morinda were usually abundant along with small breadfruit seedlings, and formed secondary forests in abandoned breadfruit groves. Openings in the canopy permitted rank growths of Wedelia biflora, the stems of which at Ine were often interlaced by the purple flowered morning glory, Ipomoea littoralis. In more completely shaded places the grasses Oplismenus, Thuarea, or Stenotaphrum covered the ground. In fact, the nearly complete ground cover in both breadfruit and coconut types -- except where the latter occurred on stony land near the ocean -- was a characteristic of these artificial forests not shared by types in which wild native trees were predominant.

At Ine the bottoms of the yaraj pits were usually occupied by the gigantic Cyrtosperma, but abandoned pits supported rank growths of Clerodendrum or thickets of Hibiscus tiliaceus. A fresh-water swamp at Tutu island formerly was planted to yaraj, but since pigs made its

culture impossible Bruguiera had been introduced.

According to Fosberg (1949) and Cox (1951), ground-water salinity is an important factor of the physical environment limiting the distribution of the breadfruit. The typhoon which swept through the eastern Marshalls in 1951 provided striking confirmation of these ideas. Although most of Arno atoll was relatively unaffected, the breadfruit groves of Bikarej were hard-hit. There many trees grew relatively close to the ocean, along the main path which extended in a north-south direction along the west side of the island. High storm waves from the west washed over the land and extended perhaps 200 feet inland. All breadfruit trees in the path of these waves were killed or severely damaged, but coconuts and cultivated varieties of pandanus were unaffected. In 1952 patches of dead breadfruits alternated with healthy bearing trees, so that it was still possible to determine at which points and how far the storm waves had washed over the land.

Weeds -

Agricultural land throughout much of the tropics is characterized by the presence of a relatively uniform weedy flora. These weeds owe their present wide distributions to the agency of man who, with modern, rapid methods of transportation, has unintentionally carried some of them to even the most remote places. Arno atoll in 1952 had about 26 species of unwanted alien weeds, most of them without well established native names or uses. Most of these had probably been introduced after 1873, when an Hawaiian mission was established at Ine. It is of interest to observe that on Arno atoll these weeds were virtually restricted to village paths and houselots. Although the breadfruit and coconut groves were maintained as such only by periodic disturbance in the form of

clearing and burning underbrush, their floras consisted almost exclusively of native species or plants of ancient aboriginal introduction. Moreover, it is a curious fact that the native herbs of coconut and breadfruit forest, with very few exceptions, did not occur in the forests of wild native trees. Thus arises the problem of the nature of their ancient, pre-aboriginal habitats, for the coconut and breadfruit groves, their present habitats, became established on Arno only after the arrival of the Marshallese.

Certain of these species were found in 1952 on open, newly formed land. Between Langar and Matolen, islands nearly obliterated in the 1905 typhoon were reforming. The following species of herbs were observed on sand freshly deposited along the lagoon shores of these islands:

Lepturus repens	Vigna marina
Fimbristylia atollensis	Wedelia biflora
Triumfetta procumbens	Cassytha filiformis

Since there is no reason to believe that typhoons were formerly any less frequent than they are now, it is extremely probable that this habitat has always been available to these species. A more extensive search would probably reveal a few other species of the ground flora of breadfruit and coconut groves -- e.g., Euphorbia chamissonis and Thuarea involuta, -- growing in similar situations. Certain species which were restricted to relatively moist, partially shaded situations may never have grown on open sandy shores. Could such plants as Centella asiatica, Hedyotis biflora, Ipomoea littoralis, and Oplismenus sp. be weeds of ancient aboriginal introduction? It would be surprising indeed if such introductions did not take place in the past as they do today. The seedless varieties of breadfruit, for example, are propagated chiefly

by root suckers. In transporting small trees from island to island the wandering Marshallese could scarcely have avoided accidental introduction of unwanted seeds in the soil around the roots. Other weeds of possible ancient introduction are Portulaca samoensis and Cyperus polystachyos, both restricted to village paths and houselots, but possessing well established native names.

SCRUB FOREST

Since the introduction of the copra trade in the latter part of the 19th century, about two thirds of the land surface of Arno atoll has been cleared and planted to coconuts. Probably at least 80 percent of the 2224 acres of Arno under coconuts in 1952 must have supported stands of wild native trees and shrubs less than 100 years before this study was made. In 1952 native forest and scrub existed chiefly in the form of numerous small stands which for the most part were restricted to situations in which copra production would probably have been relatively uneconomic. Native forest and scrub was thus characteristic of small or narrow islands remote from villages and of stony land and ramparts, especially those exposed to salt spray and the drying effect of the northeast trades. In such situations the native brush acted as an effective windbreak, protecting the coconut and breadfruit trees planted farther inland.

This wild vegetation was composed of woody plants ranging from 2 to 80 feet in height, and varying in structure from nearly impenetrable thickets of shrubs along ocean shores to closed-canopied forests of large trees through which one walked with ease. Furthermore, the type included 17 woody species, few of which were distributed over the entire

area of the type as it is mapped. In view of the great range of variation of physiognomy and floristic composition of this vegetation, it is perhaps unrealistic to consider it a single type. Largely for convenience of mapping, however, the scrub forest is here treated as a unit. It was not possible in the field to examine each of the 143 stands mapped as scrub forest, and in general the component species cannot be distinguished on aerial photographs of a scale of less than 1:5,000. Subdivision of the type based on floristic composition was thus impracticable. Furthermore, the average size of the stands of scrub forest as here presented is only 4 acres; many of these are 200 feet or less wide. Splitting of the type would have led to obvious difficulties in drafting the map.

Although the scrub forest of Arno was reduced in 1952 to numerous small stands occurring chiefly on the ocean sides of windward islands, it is perhaps possible conceptually to reconstruct the appearance of the vegetation of the atoll of the early 19th century, when perhaps only about 15 percent of the land surface of the atoll was appropriated for agriculture. Certain regularities were observed, for example, in the distributions of the native trees as one proceeded across the islands of the atoll from lagoon to ocean. Thus, large individuals of Pisonia grandis occurred on several of the windward islands from Jilang to Takleb. It is probable that these trees were relics of former forests in which Pisonia was an important species. In 1952 Pisonia also formed forests along the boulder ramparts of a few islands, but the trees were much smaller than the scattered individuals still standing inland. On the basis of such observations it is possible to construct a diagram (Fig. 12) on which are charted the distributions of the more important species of

the native woody flora across an hypothetical, relatively undisturbed atoll island. For each species the ordinate represents the author's impression of the importance of that species in the vegetation. Those parts of the figure in solid black represent trees actually observed at Arno atoll; stippled areas represent the author's extrapolations. For example, a few large Pisonia trees were observed about 300 feet from the lagoon shore of Takleb island, surrounded by young breadfruit and kapok trees. These Pisonia trees, together with other individuals observed in similar situations on other islands of the atoll, are represented in the soild black area near the lagoon shore of the hypothetical islet. The chart thus constitutes a diagrammatic conceptual synthesis of the author's observations of many stands and individual trees on several islets.

In many cases it was impossible to support these impressions of "importance" with numerical data based on sample plots, for they are based in part on the observations of the heights and trunk and crown diameters of single trees. Despite the highly subjective manner in which Fig. 12 was constructed, the author believes that it is in a sense reproducible -- i.e., that an independent investigator on Arno could construct a similar series of diagrams without having first consulted the ones here presented. Essentially, the diagrams constitute an attempt to avoid verbal descriptions of the field occurrences of trees (e.g., "Hernandia sonora: commonly encountered near lagoon shores, especially along village paths, but on Langar observed on stony land 200 to 400 feet from the ocean, where the trees attained maximum heights of approximately 60 feet.").

It may be noted from the chart that the author noted a general zonation in the flora and in the vegetation as expressed in the "importance" of the different species. Certain species, such as Scaevola frutescens and Tournefortia argentea ranged completely across the islands of the atoll, but were much more abundant and formed a larger proportion of the vegetation near lagoon and especially ocean shores. Other species, such as Pisonia grandis, Allophylus timorensis, and Pipturus argenteus, were far more characteristic of the interiors of islands, where, indeed, they attained their greatest sizes. Guettarda speciosa and Pandanus tectorius, on the other hand, were more or less ubiquitous. In general, the distributions of the species overlapped, but did not coincide. Furthermore, as is discussed below in more detail, the forest and scrub as it existed on Arno in 1952 was commonly characterized by the presence of small stands consisting of a single species of tree. It would seem unrealistic, therefore, to attempt to distinguish within the broad scrub forest type plant communities based on floristic composition. Not only did the distributions of the species making up almost any conceivable plant community fail to coincide, but very commonly the component species did not even grow together. Indeed, the author found no evidence on Arno that the native plants were distributed in such a fashion as to suggest that any of the species might be mutually dependent. Competition for light, nutrients, and water undoubtedly occurred, but such interactions did not result in apparently integrated plant communities the composition and appearance of which were relatively uniform from place to place.

Since it is unrealistic to attempt to classify the native scrub forest of Arno atoll into communities based on differences in floristic composition,

it is convenient instead to consider the variation of the scrub forest in relation to the different habitats on which it was found. The major physiographic divisions of an atoll island (at Arno) were boulder ramparts, low interiors, and lagoon shores and dunes. The low interiors may conveniently be classed into those possessing stony or sandy soils, since it is known that the salinity of the ground water of an atoll islet depends on the permeability of the materials making up its soils. When one compares such a classification of habitats with the distribution of species as presented in Fig. 12, it is evident that a general correspondence exists, although, of course, it may be objected that this correspondence is manufactured, since the diagrams are based to a large extent upon subjective impressions. Nevertheless, it is true that Scaevola and Tournefortia as important species were largely restricted to boulder ramparts and lagoon shores. Ochrosia, Hernandia, Intsia, Barringtonia, and Cordia occurred as important species only on stony land on the ocean sides of islands mostly 100 feet or more from the ocean. Pisonia and Allophylus reached their best development on the sands of island interiors. The following descriptions of the native forest and scrub, then, are basically descriptions of the "scrub forest" vegetation as it occurred on the different "natural areas" of the atoll.

BOULDER RAMPARTS

Primary species: Scaevola frutescens

Secondary species: Tournefortia argentea
Guettarda speciosa
Terminalia samoensis
Pandanus tectorius
Cocos nucifera
Pemphis acidula

At Arno coconut plantations very commonly extended to the tops of boulder ramparts of the ocean shores of leeward islands. The proportion of wild woody shrubs in the understories of these groves commonly increased toward the ocean shores, and thickets occurred in neglected plantings. On ocean shores exposed to the full force of the prevailing northeast trades -- e.g., Bikarej, Langar, and the chain of islets extending between them; Ijoen; and the northern tip of Matolen -- native shrubs and trees formed belts of vegetation on the tops of the boulder ramparts and extending inland in places 200 feet or more.

In most such situations the primary species of the vegetation of the tops of boulder ramparts was Scaevola frutescens. Thickets of this species in places extended about 75 feet inland from the ramparts, increasing in height from one foot at their outer margins along the stony beaches to fifteen feet where they merged with the forests of larger native trees in the interiors of the islands. These thickets were in effect sloping hedges, consisting of an unbroken layer of large, fleshy leaves supported by innumerable upright branches. Although such thickets were not literally impenetrable, they were exceedingly difficult to traverse and have been aptly termed "beach barriers" by Mr. E. H. Bryan. Tournefortia argentea, Guettarda speciosa, and Terminalia samoensis usually grew among the shrubs of Scaevola, in places partly replacing them over small areas.

STONY INTERIORS

Primary species:
- Pandanus tectorius
- Ochrosia oppositifolia
- Guettarda speciosa
- Tournefortia argentea
- Cordia subcordata
- Intsia bijuga
- Allophylus timorensis
- Pisonia grandis

Hernandia sonora
Barringtonia asiatica
Cocos nucifera

Secondary species: Terminalia samoensis
Scaevola frutescens
Pipturus argenteus
Soulamea amara

Ground layer: Asplenium nidus
Polypodium scolopendria
Peperomia sp.

Lianas: Ipomoea tuba
Wedelia biflora

Epiphytes: Asplenium nidus
Nephrolepis sp.

Height of Canopy: 15 to 60 feet; mostly 25 to 35 feet.

Density: 100 to 300 or more trees per acre over 1 inch d.b.h.*

A forest in which 14 species of native trees occurred was commonly encountered on the stony soils of windward islands immediately inland from the beach-barrier scrub of Scaevola frutescens. The width and development of this forest appeared to be largely dependent upon the extent of human activity. Where the land was remote from human habitation, too narrow for effective crop production, or possibly in areas of disputed land ownership, the zone of native forest was in places 300 or more feet wide. In such situations as one proceeded inland the size of the trees increased until individuals of Pisonia, Intsia, Barringtonia, Hernandia, or Ochrosia might attain heights of 50 to 60 feet and trunk diameters of 20 inches or more. The average diameter of the trees over 1 inch d.b.h. in one Ochrosia stand, was 14.4 inches

* diameter at breast height.

(Basal area: 164 sq. ft/acre; density: 150 trees/acre). To walk into such a forest from the ocean reef flat was to step into a different world. The light intensity fell to only 2.5 percent of the glare obtaining on the reef flat. One was immediately conscious of numerous coconut and large hermit crabs; the former usually scuttled rapidly to holes excavated in the purple-brown phosphatic sand between the stones and cobbles of the forest floor. At the approach of an intruder, the terns roosting and nesting in the trees set up a hoarse clatter. Where the bird's nest fern, Asplenium nidus, grew among the fragments of coral rock, its enormous leaves -- to five feet long -- were often conspicuously spattered with the white droppings of these birds. Here and there patches of Peperomia formed small "rock gardens" under the trees. Elsewhere, however, the ground was quite bare of plants other than the slippery algae covering the rock fragments. Tree seedlings were usually not conspicuous.

On the windward islands these forests reflected in their growth the prevailing direction of the wind. The canopy of the forest and of the Scaevola scrub to windward was in effect a plane of leaves dipping toward the ocean beach at angles of 9 to 13 degrees. On Langar, Barringtonia and Hernandia were predominant in a small portion of the native forest. These trees appeared to have been restricted in their upward growth by the salt-laden winds, for although they were massive, with trunks over 2 feet in diameter, many were scarcely 25 feet tall. Their trunks were inclined at dangerous angles or actually prostrate on the ground, and branches projecting above the canopy of the forest were mostly leafless. The grotesque shapes of trees suggested the fanciful thought that failing in their struggle to pierce an invisible barrier above them, they grew horizontally instead of vertically in a claustrophobic attempt to escape

from the inadequate space within which they were confined. Farther inland, however, Hernandia trees of the same stand were erect and attained heights of 60 feet or more.

An interesting feature of these forests, probably to be attributed to accidents of distribution of propagules, was the tendency of the component species to form alternating nearly pure stands averaging perhaps 0.1 acre in area. In walking parallel to the shore, one might pass from dar patches of Ochrosia forest into sunny open stands of Pandanus tectorius, and from these into thickets of Guettarda speciosa or Allophylus timorensis. Here and there were observed groups of five and six small Soulamea trees. Elsewhere, as on Takleb island, groups of tall Intsia or Pisonia occurred, or the heavy branches of Cordia subcordata leaned to the ground and struck root, giving rise to thickets of that species. These alternations of single-species dominance occurred with no regularity, nor did there appear to be any marked tendency for one species to replace another. It is true that seedlings and saplings of Ochrosia oppositifolia were conspicuously vigorous when growing in heavy shade, but a high proportion of the large fruits of this species failed to germinate among the stones and cobbles of the forest floor, and there would seem to have been no agency other than heavy storm waves by which these awkward propagules might be carried from place to place. Guettarda speciosa, and the coconut, however, were ubiquitous, and old trees of Tournefortia argentea occurred in scattered fashion throughout the forest.

Stands of large Hernandia, Barringtonia, Ochrosia, Pisonia, or Intsia were rather exceptional. More commonly the native forest consisted of thickets, sometimes containing several sprouting cut stumps,

immediately behind the ocean beach barrier of Scaevola frutescens. In such situations the most common trees were Pandanus, Guettarda, and Tournefortia, the latter two with short, thick, crooked boles, sending out many low, spreading branches. Terminalia samoensis and Scaevola frutescens were also abundant, and such lianas as Ipomoea tuba and a scendent form of Wedelia biflora bound some of these thickets into nearly impenetrable tangles.

SANDY INTERIORS

Primary species: Pisonia grandis
Allophylus timorensis
Cordia subcordata ?
Intsia bijuga

Secondary species: Pipturus argenteus
Premna obtusifolia
Guettarda speciosa
Pandanus tectorius

Ground layer: Polypodium scolopendria

Height of Canopy: 20 to 80 feet

Density: 15 to 300 trees per acre over 1 inch d.b.h.

In 1952 3 massive Pisonia trees stood in the middle of Takleb island, surrounded by a forest of small kapok and breadfruit trees. The largest of the Pisonias was about 80 feet tall and 28.4 feet in circumference. Other large, isolated Pisonia trees were observed in the interiors of Enidrik and Jilang islands. Since it appeared possible that these trees might be remnants of the native forests which must have once covered the interiors of these islands, the writer questioned Felix J., the magistrate of Arno atoll in 1952, whose family holds land rights on Takleb, as to this history of Takleb. He very kindly offered the following data:

Until 1876 Takleb island was an "island of birds," i.e., a royal

bird reservation upon which trespass was forbidden (c.f. Tobin, 1952). Periodic visits were made by authorized collectors to gather birds and eggs. In 1876 the prohibition against visiting Takleb was removed, and around 1886 Tobikle, a "brother" of Felix*, having obtained rights to the use of the land, commenced to clear the wild forest and plant breadfruit and coconut trees. Felix stated that the original forest of the interior of Takleb did not consist exclusively of Pisonia trees. Rather, the Pisonias occurred in two groups, which alternated with pure stands of Allophylus, Intsia, and Cordia. Species of birds not present at Arno in 1952 and not reported by Marshall (1951), including the "ak" (frigate bird), "nana," and "kalo," roosted in the trees, together with many terns ("rabit," "jakar", etc.). The rookery was evidently much larger than any remaining on Arno atoll in 1952. The kapok was introduced in 1915, seed having been sent from Ponape.

Felix's account was confirmed by Tobu, the paramount chief of Arno in 1952, who added that Namwi island had also been an island of birds until 1876, when the iroij, Lekaman, removed the emo (tabu) from both Takleb and Namwi. The writer encountered numerous small Pisonia trees in the interior of Namwi, growing on phosphatic sand and rock. All appeared to be of sprout origin. In view of the very great powers of vegetative reproduction possessed by Pisonia grandis, I consider it quite likely that the stand of sprouts and suckers observed on Namwi in 1952 consisted of the same trees which grew there before 1876 and

* The term "brother" in the Marshall Islands is apparently applied to all male relatives of the same generation as the speaker. Thus, Tobikle may have been Felix's cousin.

that these trees then formed a high forest over much of the phosphatic area of that island.

In spite of its decimated character in 1952, the remnant of the Pisonia forest was most striking. The pre-1876 groves of Takleb and Namwi must have been impressive. On the basis of my observations of the Takleb trees the following reconstruction may be hazarded.

The forest was composed almost exclusively of old trees of Pisonia grandis between 3 and 9 feet in diameter at breast height and 75 to 85 feet tall. Assuming that the canopy was about 90 percent closed, the density of stocking was about 15 trees per acre. The forest floor was essentially bare of tree seedlings or herbaceous plants, but leafy root suckers of the Pisonias must have been conspicuous. Thousands of birds perched in the branches of the trees and the air resounded with their raucous cries. Their droppings combined with the decaying leaves of the Pisonia trees to form a black, mucky humus resembling the greasy mor type of the humid temperate regions. Over and through this humus crept the serpentine roots of the Pisonias, only occasionally penetrating to depths of more than one foot. Phosphatic salts leaching from the humus stained the pinkish limesands beneath a purple-brown and with the subsequent precipitation of calcium phosphate, phosphatic rock was formed. This phosphatic hardpan was in some places able to perch a water table, so that small pools persisted on the ground after heavy rains. In places where the rock had not consolidated completely, however, rainwater percolated through the sandy soil to the permanent ground-water table more than four feet below the surface of the soil.

Typhoons left their mark on this forest, although they did little to alter its composition. The tops of the great trees in some cases

were broken off, at times 10 to 20 feet above the ground, and some trees were completely uprooted. These trees, however, were not all killed. From broken trunks and creeping roots numerous quick-growing suckers arose, quickly filling the gaps in the canopy. Fallen logs developed roots along much of their length, and rapidly growing sprouts along their upper surfaces later developed into trees which in 1952 seemed to be growing in rows, as if planted. Even fallen branches struck root and developed into trees where the light intensity was sufficient.

In 1952 Pisonia grandis was considered a major pest and had been eradicated as an important species from all islands of Arno atoll except Takleb, Takleb ej, Enidrik, Jilang, Namwi, and Langar. In addition, lone Pisonia trees stood at Matolen and on Arno island. Habitats which appeared suitable for the species, however, occurred in the secondary forest of Arno island as well as on Ijoen and other islands reforming between Malel and Matolen, following the typhoons of 1905 and 1918. The sticky fruits of the Pisonia adhere to the feathers of birds roosting and nesting in its branches, and are believed thus to be carried from island to island. Evidently this mechanism of dispersal is not very effective in the short run. A careful search for trees of undoubted seedling origin revealed only a few, although sprouts and suckers were abundant. Once established, however, the tree seemed to be almost immortal. The virtual indestructibility of the older trees -- fire is the only effective means of clearing Pisonia forest -- combined with their great powers of vegetative reproduction seems to be sufficient to account for the

former predominance of Pisonia on parts of Takleb and Namwi. It is possible that these trees were members of clones resulting from the chance long-distance dispersal and establishment of single seeds.

The groves of Allophylus, Cordia, and Intsia, which according to Felix shared the interior of Takleb island with the Pisonias, were reduced in 1952 to a few trees growing on stony soil near the ocean side of the island. Of these Intsia is the largest tree, attaining a trunk diameter of 19 inches, and heights of over 60 feet. Cordia subcordata is a much more compact tree than Intsia bijuga; on Arno atoll it reached heights of 45 feet. Its crowns were mostly wide-spreading and its thick branches originated low on the main bole, which attained a maximum diameter of 28 inches. Allophylus timorensis was common in the interiors of Arno and Langar islands. It was never taller than 30 feet, and its trunks were mostly slender whips.

LAGOON SHORES AND DUNES

Primary species: Scaevola frutescens
Pemphis acidula

Secondary species: Suriana maritima
Sophora tomentosa
Guettarda speciosa
Pandanus tectorius
Tournefortia argentea
Cordia subcordata
Barringtonia asiatica
Terminalia samoensis
Hernandia sonora (planted?)
Callophyllum inophyllum (planted)
Hibiscus tiliaceus (planted)

Herbaceous pioneers: Lepturus repens
Vigna marina
Wedelia biflora
Triumfetta procumbens
Fimbristylis atollensis

Between Lukwoj and Jabu, on the long southern island of Arno atoll, and on several of the islands devastated by the typhoons of 1905 and 1918 between Langar and Matolen native forest and scrub occurred along lagoon shores. The primary species in such situations were Scaevola frutescens and Pemphis acidula. The latter commonly formed pure stands where the beach was composed of sandstone or consolidated fragments of reef rock. At high tide the Pemphis trees often overhung the lagoon, so that when traveling along the beach one frequently was forced to wade around the trees or detour inland.

Pemphis also occurred on unconsolidated sands and dunes along lagoon shores, together with Scaevola and, near Lukwoj, Suriana maritima. Cordia subcordata, Terminalia samoensis, Pandanus tectorius, Guettarda speciosa, and Tournefortia argentea were other trees frequently encountered on sandy soils near the lagoon. In villages Hernandia sonora and Calophyllum inophyllum were common. Rainwater running down the trunks of the latter was often collected in large iron drums.

SALINE FLATS

Primary species: Pemphis acidula

Secondary species: Scaevola frutescens
Tournefortia argentea
Bruguiera conjugata

Small interior saline flats occur on several islands of Arno atoll. Commonly these had the form of elliptical, flat-bottomed depressions about 200 feet long and 50 feet wide. Island sandstone was exposed in the bottoms of some of these depressions; drifting sand had accumulated in others. At high tide saline ground water might rise above the level of the bottom of the flat, or where a channel opened to the ocean or

lagoon, salt water washed in with the tides. Commonly at low tide small pools were found in depressions in the flats and the water in these was salty to the taste.

The slightly higher rim of such flats was composed commonly of consolidated rock, and on this rock as well as on islands of sand or rock within the flat itself occurred nearly pure stands of Pemphis acidula. The Pemphis is a large shrub or small tree 15 to 25 feet in height. Its exceedingly hard, heavy wood, which sinks like a stone in salt water, was prized as a source of durable construction timbers and coconut husking sticks; formerly it was the preferred wood for spears. Where sand had filled the bottoms of the flats, Scaevola frutescens and Tournefortia argentea together with the Pemphis formed open stands.

The largest of the saline flats of Arno atoll was found between Bikarej and Badrbaren islands. There, on low islands between tidal channels and pools, the Pemphis formed essentially pure stands. At high tide salt water washed over its exposed roots and those covered by sand were undoubtedly bathed in the saline ground water. Fiddler crabs had excavated innumerable holes in the muddier portions of the flat, and permanent pools a few inches deep were inhabited by gobies, which darted into holes or under sheets of algae when disturbed.

At Bikarej, Namwi, and Enidrik islands Pemphis bordered mangrove swamps. It differed from the mangroves,* however, in that whereas the latter were restricted to swamps in which peat formed under water, Pemphis was most abundant on sites which at low tide appeared to be well drained and even dry. Small depressions in beach conglomerate formed along lagoon shores constituted an especially common habitat.

* Sonneratia, Bruguiera, Lumnitzera (Combretaceae).

MANGROVE SWAMPS

Primary species: Bruguiera conjugata

Secondary species: Sonneratia caseolaris

Lumnitzera littorea

Pemphis acidula

Epiphytes: Asplenium nidus

Nephrolepis sp.

Density: About 90 trees per acre over 6 inches DBH, but variable.

Height of canopy: 35 to 55 feet.

The principal areas of occurrence of mangrove swamp were Tinak, Langar, Bikarej, and Namwi Islands, and the districts of Kinajong and Matolen, on Ine Island. Elsewhere stands consisting of one to a few trees may grow in local depressions. The swamps were of two kinds. The more common type was the interior swamp or "bat," cut off from any connection with the lagoon or ocean by dunes on the lagoon sides or by boulder ramparts on the ocean shores. Certain of these interior muddy depressions apparently resulted from the formation of successive boulder ridges of coarse rock on the ocean sides of islands.

The less common ("jinbatbat") type of mangrove swamp occurred at Bikarej and Namwi Islands, bordering the enclosed North Horn lagoon. On both of these islands shallow embayments opened on the lagoon. The swamp at Namwi, however, had been cut off from the lagoon by sand which drifted across the outlet. Drifting sand had also covered the center of the Namwi embayment forming a salt flat on which grew scattered shrubs of Pemphis and Scaevola. The connection of the Bikarej swamp

with the lagoon was still open, and water ran in and out of the embayment with the tides. During the day at low tide this water became extremely hot, and evaporation probably tended to increase its salinity appreciably. Brine shrimp were abundant.

In both places the mangrove trees formed merely a bordering ring around the interior flat. Scattered, mostly prostrate trees of Sonneratia caseolaris, which on Arno atoll was restricted to the Bikarej and Namwi swamps, bordered the central flats of sand or mud; their erect, conical pneumatophores extended twenty feet or more beyond the main boles of the trees toward the center of the embayment. Behind the Sonneratia trees and tending to fill the gaps between them occurred the more erect Bruguiera conjugata, perched upon which were aerial baskets of Nephrolepis and Asplenium. Seedlings of Bruguiera also became established in the mud beyond the Sonneratias, but they were apparently short-lived in such situations. Forming a zone around the Bruguiera were thickets of Pemphis acidula, the sprawling main trunks of which sent up erect branches 15 to 20 feet in height and over 6 inches in diameter. Behind the Pemphis occurred trees of the scrub forest (especially Intsia and Allophylus), impenetrable thickets of Clerodendrum inerme, or coconut plantations.

Mangrove swamps of the interiors of islands were strikingly difference in appearance. Instead of a mere ring of trees bordering a barren embayment or flat, a complete cover of trees occupied the inland swamps. Most of these stands contained only a single species of tree, Bruguiera conjugata. Only at Matolen did Lumnitzera littorea, prized for fishing poles and garlands, grow with the Bruguiera. Thickets of the attractive white-flowered Clerodendrum, also used for garlands,

sometimes bordered these interior swamps.

Mangrove swamps of the interiors of islands varied considerably in density of stocking, distribution of diameter classes, and form of the larger trees. At Tinak and Kinajong the largest trees were mostly tall and straight, and the distribution of mature trees, young poles, and saplings, was relatively uniform throughout the swamps. The largest trees at Kinajong were 50 feet or more in height and about two feet in diameter at breast height. The trees at Tinak were somewhat smaller, but the proportion of tall, straight trees which had pruned themselves of their lower branches was higher.

The case was different at Matolen and Langar. In those places the stands consisted of scattered groups of old trees of poor form alternating with groups of younger, straighter poles. A dense growth of Bruguiera seedlings about 18 inches tall constituted the ground layer, and the bird's-nest fern grew perched on the larger trees. Seedling mortality of the Bruguiera was probably high in the heavy shade, for the density of poles 10 feet or more in height was much reduced.

The poor form of the older trees at Langar and Matolen, which were about 35 to 45 feet tall, exceedingly crooked, and commonly with heavy branches originating less than 10 feet above ground, indicates that they must have grown under conditions very different from those obtaining in 1952. Their offspring, growing densely under partial shade, had developed into tall, straight, slender poles which had pruned themselves of their lower branches. This suggests that the mangrove forests of Langar and Matolen might have been of very recent origin. The older, poorly formed "wolf" trees must have grown in

openings as scattered individuals and small groups. Those parts of the swamps occupied in 1952 by young poles were probably also open prior to the establishment of the latter, for the stocking was dense and uniform and the trees were of nearly identical size, diameter, and form. It is not impossible, of course, that such local openings could have resulted from the uprooting of patches of a former forest during typhoons, but no evidence of typhoon damage in the form of fallen logs partially or wholly buried in the peat could be found; the 1918 typhoon, in which many breadfruit trees were uprooted on Langar, is said to have caused no appreciable damage to the mangrove forests of that island. "High-grading," that is, the practice of harvesting the more desirable trees whilst leaving behind those of poor form, may have contributed to the preponderance of wolf trees among the older age classes. In 1952, however, cutting methods consisted of removing only a few of the better formed poles. In the terminology of the forester, this constituted merely a "light thinning." Clear cutting was not practiced in 1952 on Arno atoll, and perhaps never was. Thus, previously existing open places of considerable size probably cannot be attributed to typhoons or former cutting practices. It seems at least possible, therefore, that the mangrove forests of Langar and Matolen originated in relatively open, swampy depressions with the establishment of the present wolf trees. When these trees reached maturity, their fruits were scattered thickly throughout the swamp, giving rise in openings to the present dense stands of poles. In other words, the mangrove forests of Langar and Matolen swamps may be no older than the wolf trees still growing in them.

Dr. Harold St. John had suggested to the author that certain of the

interior mangrove swamps might have originated through the deliberate introduction on the part of the Marshallese of fruits of the Bruguiera into open swamps. One clear case of artificial introduction and establishment of Bruguiera was actually encountered, suggesting that at least some of the existing interior Bruguiera stands of Arno atoll may have originated in this way.

On Tutu Island a fresh water swamp was encountered (chloride concentration 15 ppm, less than 0.1% of that of the local seawater), in which several young trees of Bruguiera were growing. The known history of this swamp illustrates the possible origin of other inland mangrove forests. Yaraj (Cyrtosperma) was formerly grown successfully in the Tutu swamp, but the rooting of pigs made its culture impossible, and Bruguiera, previously absent, was deliberately introduced some time between 1933 and 1942. In 1952 there were at least two age classes present. The older, larger trees, growing in openings among taller coconuts and pandanus, were of distinctly bushy habit, and seedlings of Bruguiera were scattered throughout the swamp. The Bruguiera plants were perhaps not so vigorous as those growing in more saline environments, but they were surviving and reproducing and may well tend eventually to displace the other species of trees now present. If this in fact occurs, a stand will be formed consisting of scattered groups of old Bruguiera trees of poor form, originating from hands full of fruits casually tossed into the swamp from points along its margin, alternating with dense growths of young saplings and poles. The stands of Langar and Matolen had precisely this appearance in 1952, so that similar origins are not impossible. It may further be conjectured that as the old, poorly formed trees of

Langar and Matolen die, they will be replaced by their taller, straighter progeny, giving rise to stands such as were seen in 1952 at Tinak and Kinajong. The relative antiquity of the stand at Kinajong is further suggested by the fact that the place name is evidently derived from "jong," the Marshallese name for Bruguiera. That is, the mangrove swamp is probably older than the name of the district, if the latter was in fact named for it.

It is of course possible that certain Bruguiera swamps of the interiors of islands became established through natural agencies alone. High storm waves washing over the land may have carried Bruguiera fruits into previously existing interior swamps, or stands of Bruguiera formerly growing along lagoon or ocean shores may have been cut off inland by the formation of new dunes or boulder ramparts. The writer, however, walked the entire southern lagoon shore of Arno atoll from the northern end of Arno island on the west to the northern end of Langar on the east without observing a single plant of Bruguiera growing in such situations. In traveling among the northern islands of the atoll he noted Bruguiera growing along lagoon shores only at Bikarej, where scattered trees extended out from the interior embayment along the northern lagoon shore of that island. Nor was Bruguiera observed growing along ocean shores, although a special search was made for the tree in such situations.

It is a common impression that mangrove swamps are invariably saline or brackish. Such was certainly not the case in the stand developing at Tutu, where the chloride concentration of the swamp water was only twice that of the local rainwater. Analyses of the

water in the Matolen Bruguiera-Lumnitzera swamp demonstrated a chloride concentration of only 640 ppm, about 3 percent of that of the local seawater. The water of the Tinak swamp, however, was distinctly salty to the taste, and at high tide the water of the Bikarej swamp mixed freely with that of the North Horn lagoon. Obviously, then, Bruguiera is capable of growing in swamps having an extremely wide range of salinity. Consequently, it should never be assumed in the Marshall Islands that the presence of Bruguiera is positive indication of high ground-water salinity.

In passing, it should be noted that large numbers of fish-eating seabirds roosted and nested in the Bruguiera trees of the Langar and other Arno swamps. The high phosphate content of the Arno mangrove peats (Stone, 1951) may be conveniently explained by their presence.

FRESH-WATER SWAMPS

Primary species: Pandanus tectorius

Secondary species: Cocos nucifera
Hibiscus tiliaceus
Intsia bijuga
Morinda citrifolia
Allophylus timorensis

Ground layer: Eleocharis sp.
Dryopteris goggilodus
Polypodium scolopendria

Epiphytes: Polypodium scolopendria
Nephrolepis sp.
Asplenium nidus

Fresh-water swamps or bogs were observed on Ulien, Tutu, and Arno islands. Of these the Ulien swamps were the largest and most

interesting. A series of swamps alternated with higher ridges composed of coarse fragments of reef rock. Perhaps the most remarkable feature was a small pond, about 100 feet long and 20 feet wide, which contained knee-deep standing water when visited. This water was fresh to the taste, and apparently not saturated with calcium or magnesium salts, for Stone (1950) stated that soap could be used. Much more shallow standing water occurred in other swamps on Ulien; on still others peat was exposed above the ground-water level. The Tutu swamp contained shallow standing water, but certain small areas in the northwest part of Arno island were merely wet underfoot. Included here also are the abandoned yaraj pits of Arno island, for their vegetation was very similar.

The predominant tree in all these swamps was the wild variety of Pandanus tectorius, "Erdwan." The trees were mostly about 35 feet tall, but density was variable, depending to some extent, at least, on the depth to the ground water. Thus the small bog surrounding the Ulien pond supported an open stand of Eleocharis. Polypodium and young Pandanus formed a zone around the sedge, followed by a belt of larger Pandanus and finally, on the higher, drier land, by coconut forest with an understory of scattered Pandanus. In the swamp west of this stand occurred both dense dark stands of Pandanus, containing perhaps 250 trees per acre and much more open stands of probably half the density of the former. The more open stands occurred on a fibrous peat which smelled strongly of hydrogen sulfide, whereas the substrates of the dense stands were dark mucks. Coconuts had been planted in many of these swamps. When windthrown, their root systems tore up patches of peat,

exposing the standing water beneath. Intsia, Morinda, and Allophylus occurred on slight rises, and Hibiscus tiliaceus, elsewhere common in abandoned yaraj pits, grew along the margins of the swamps. Eleocharis was abundant in open places in the Ulien and Tutu swamps, but was not seen on Arno island. As noted by Stone, Dryopteris goggilodus grew in open places in the abandoned yaraj pits of Arno, but apparently did not occur elsewhere on the atoll. This suggests that it may have been of accidental aboriginal introduction, spores possibly having adhered to the corms of Cyrtosperma. On the dry exposed peat west of the Ulien pond Lepturus repens formed bunches, and Fimbristylis atollensis was common on slightly higher situations.

The history of the vegetation of the Ulien swamps and the surrounding higher land might well be worth intensive study by the methods of pollen analysis.* Such a study would necessarily include an account of the origin and age of the swamps and the unique pond. It is suggested here that these interior depressions are of natural structural origin, the result of the formation of successive boulder ridges on the ocean side of the island, possibly as the reef grew outward. At least one such interior boulder ridge contained a thicket of Scaevola frutescens similar in all respects to the brush of that species which so commonly borders ocean shores. On the other hand, my informants confirmed the legend related to Stone that an Ulien retting pit was excavated by a star.

* A radio-carbon analysis of the layer of peat in which breadfruit pollen first appears might give a minimum date of the occupation of Arno atoll by the Marshallese.

It would seem improbable, however, that the Ulien swamps were formed by a shower of meteorites.

Secondary Forests of the Interior of Arno Island

Primary species	Ground layer
Allophylus timorensis	Tacca leontopetaloides
Artocarpus altilis	Polypodium scolopendria
Premna obtusifolia	Nephrolepis sp.
Guettarda speciosa	Asplenium nidus
Pandanus tectorius	Crinum asiaticum
Cocos nucifera	Dryopteris goggilodus
Ochrosia oppositifolia	(abandoned yaraj pits)

Secondary species

Randia cochinchinesis
Scaevola frutescens
Ipomoea tuba
Hibiscus tiliaceus
Morinda citrifolia
Ixora casei
Pipturus argenteus

In 1952 a considerable part of the interior of Arno island was occupied by a growth of small trees, of which Allophylus timorensis was the most abundant. Growing with the Allophylus and often locally predominant were Guettarda speciosa, Premna obtusifolia, and Pandanus tectorius. An aggressive seedless variety of the breadfruit, "Bukaral", maintained itself in these forests by root suckering; a seeded variety, "Mijwan," was also present but less common. The main, closed canopy of the forests was 25 to 35 feet above the ground, but breadfruits and coconuts 40 to 50 feet tall occurred scattered throughout. Randia cochinchinesis, resembling a small coffee tree, was common in the shrubby layer, and Tacca, Crinum, and seedlings of Allophylus were conspicuous on the ground.

Although the relative abundance of the component species of trees

was spatially variable, their sizes in general were not. The breadfruits were mostly 6 to 10 inches in diameter and lacked buttressed roots. The Allophylus trees were slender whips, 2 to 4 inches in diameter, and the Guettarda was scarcely larger. The small size of the trees suggested that these forests were not old. This supposition was confirmed by the presence in the forest of abandoned house sites, around which Ixora bloomed profusely, and yaraj pits, occupied by rank growths of the wild pandanus ("Erdwan"), Hibiscus tiliaceus, and Dryopteris goggilodus. These secondary forests clearly had grown up in land formerly utilized for agriculture.

An attempt was made to determine the history of land abandonment on Arno. According to several informants, Arno island was once the headquarters of a powerful prince, Lojette, who is said to have conquered seven atolls of the Radak chain and to have originated such institutions as a military school and a corps of physicians. After Lojette's departure from Arno dissension broke out among his followers; wars, famine, and disease are supposed to have decimated the population.

Much of the history of Lojette is undoubtedly pure myth. On the other hand, Lojette is listed on the register of the iroij lablab of Arno kept by Lajibili, the former magistrate of the atoll, and Lojette's descendants are among the nobility of Maloelap and Majuro. The ruling tribe of Jebrik and Kaiboke at Majuro, for example, traces its descent to Lojette and his second wife, Liwarelik, a member of the Rarno clan. The geneology of at least one descendant of Lojette, Karjin of Ailok, is known accurately and serves to place the date of birth of Lojette between 1720 and 1780.*

* Lubne X Lojette → Limajjen → Neikom → Lekam → Lajen → Litoene → Karjin, about 50 years old in 1952. Length of generation: 20 to 30 years. Informant: Raymond de Brum.

Jon, an old man of Arno island, kindly showed the author the site of a house which he said was occupied by Lojette and permanently abandoned after his departure from Arno. Excavations revealed that the depth of accumulation of coral pebbles in the ancient courtyard varied from 12 to 19 inches. Pebbles in courtyards of known age were found to accumulate at the rate of about one inch every ten years. Thus the housesite had been occupied roughly 120 to 190 years at the time of abandonment. If Lojette was 40 to 70 years of age when the house was abandoned, then it was first occupied sometime between 1570 and 1730. Many abandoned courtyards were found inland from the one said to have been occupied by Lojette. Most of these belonged to the commoners (kajur), who cultivated the nearby yaraj pits and harvested the breadfruit.

The interior of Arno island was probably inhabited until about 1860 or 1870. Lajibili, who is now about 60 years old, stated that Arno island consisted of 3 inhabited districts during the time of his grandfather -- ocean and lagoon shores and the interior. During the time of his father only the ocean and lagoon shores were inhabited, and in 1952, except for a single interior house, dwellings were restricted to the path near the lagoon shore. Yaraj was grown in the now-abandoned bwil (pits) during the time of the Japanese (1914-1944), but rooting by pigs had resulted in the abandonment of almost all yaraj pits before the arrival of the Americans; I saw only one pit on the island which still contained Cyrtosperma.

The Arno people attributed the abandonment of housesites in the interior of Arno island to a simple decrease in the human population. About 200 people lived on Arno in 1952, but many of these were relatively recent immigrants from Mille, Wotje, and Majuro. A former larger

population is certainly not impossible. Much more food must have been produced before the yaraj pits were abandoned. On the other hand, a simple migration of biological families from the interior of the island to the lagoon shore may have taken place with no change in the total population of the island. The writer observed abandoned housesites similar to th Arno ones in the interior of Ebon island, Ebon atoll. He was informed by Dwight Heine, a resident of Ebon but superintendent of schools at Majuro in 1952, that at Ebon "ri jerbal" formerly occupied the less desirable interior houses, lagoon shore sites of the watos having been reserved for the alabs. At Ebon and Arno all the members of a bwij in 1952 lived in a group of houses conveniently near a commonly shared cook house near the lagoon side of the wato.

If the population of Arno island was formerly considerably larger than it was in 1952, the interior -- the area of secondary forest and much of the land under coconuts -- may have resembled that of Majuro island in 1952, where interior houses set among large breadfruit trees were still occupied. The yaraj pits were maintained; bananas and limes were abundant; and the underbrush was kept more or less in check.

If, on the other hand, the population of Arno has not changed appreciably and the biological families constituting a bwij were formerly scattered in a line running from ocean to lagoon, wild native trees may have made up an appreciable part of the vegetation. Perhaps only a small area around each house was kept relatively clear of brush. It should be emphasized, however, that in the Marshall islands it is not possible to make a sharp distinction between agricultural and waste land. Management consists chiefly in cutting back competing unwanted wild vegetation.

Intensively managed coconut and breadfruit groves are parklike. On the other hand, breadfruit, yaraj, and coconuts are harvested in jungle-like areas which might well be mapped as secondary forest. The degree of neglect varies from wato to wato. It is not unusual to find a strip of land almost completely devoid of underbrush bordered on both sides by nearly impenetrable thickets of small native trees overtopped by coconut or breadfruit trees.

At about the time of abandonment of the interior dwellings on Arno, German traders commenced buying copra in the Marshall islands. Gradually land under native scrub and unneeded breadfruit forest was cleared and planted to coconuts. Although the new coconut plantations were generally successful near ocean and lagoon shores, the conversion met with difficulty in the interiors of the widest islands of several atolls in the southern Marshalls. After a few productive years, the trees effectively ceased bearing and many died. In 1952 a few Arno landholders continued to maintain their failing groves, whereas others had abandoned the attempt to produce copra in the interior of the island. How much of the present secondary forest followed directly in the wake of the failing coconuts is not known. Probably some breadfruit land passed to secondary forest without first having been planted to coconuts, the older breadfruit trees having been salvaged for canoes.

In 1952 some areas of poor coconuts were being invaded directly by breadfruit trees, especially the variety "bukaral." More commonly the earliest invaders were Wedelia and Premna, the latter forming thickets of whippy stems six to nine feet tall. A representative zonation was observed in the wato Mwun Karel near the ocean side of the secondary forest.

The sequence was (1) poor coconuts with Fimbristylis and a black alga prominent on the ground; (2) Wedelia; (3) 6-foot Premna; (4) Pipturus argenteus with an undergrowth of scattered Thuarea; (5) Randia cochinchinensis and Morinda citrifolia over which Ipomoea tuba climbed; (6) 12-foot Guettarda; and (7) closed forest of Pandanus, Allophylus, Premna, and Guettarda.

In the closed forest Allophylus, young trees of which were abundant on the forest floor, appeared to be increasing at the expense of Premna and Guettarda. Seedlings and saplings of the Premna were never observed growing under closed secondary forest, and small Guettarda were common only in openings and at the edge of the forest. Ochrosia oppositifolia, a rare species except near ocean shores, occurred in abundance at one place in the interior of Arno island. It appeared to be the only species on the atoll capable of growing in its own dense shade. The area under Ochrosia is not likely rapidly to increase in size, however, for the Ochrosia fruits are large and heavy and are not usually disseminated far from the parent tree. The same may be said for the fruits of Hernandia sonora. A single large Hernandia was found in a patch of secondary forest near the ocean side of Arno island, but seedlings were observed only within 50 feet of the trunk of the parent tree.

Secondary forest on Arno occurred on Arno loamy sand. According to Stone, these soils were formed "under a native mixed broadleaf forest that was replaced in part by the indigenous agriculture and more or less completely by 'copra culture.' Thus their development cannot be related to the existing vegetation." The present author, however, encountered an immature Arno soil on the rim of an excavated yaraj pit in the breadfruit

forest near Ine village, suggesting that the series can develop under breadfruit trees. It appears fairly certain that a large part of the area of Arno loamy sand on Arno island, including the present secondary forest, was under a form of indigenous agriculture for at least 130 to 300 years before the advent of "copra culture." The history of use may be much longer. Since the Arno loamy sands occur chiefly in the interiors of the wider islands -- the regions best suited for breadfruit and yaraj culture because of the low salinity of the ground water, it is not unreasonable to postulate that the areas under soils of the Arno series in 1952 were among the first to be occupied by the Marshallese voyagers upon their arrival at the atoll. With the establishment of the Marshallese agriculture, the soils were disturbed by the excavation of yaraj pits. The uprooting of trees during typhoons and lesser storms has been another factor tending to obscure the original soil.

It should further be emphasized that there is no field evidence that the interior of Arno island was ever occupied by a native mixed broadleaf forest. Present stands of wild native trees infrequently visited by humans are commonly characterized by the presence of seabirds and phosphatic sands or rock. Phosphatic areas indicative of former flocks of roosting and nesting seabirds were entirely lacking on Arno island. Indeed, Stone's analysis of a sample of Arno loamy sand from the area of poor coconuts on Arno showed a surprisingly low content of available phosphorus in the black surficial horizon. He reported only 10 pounds per acre, about 10 percent of that obtaining in the productive groves.

VEGETATIONAL CHANGE

Processes of large-scale change in the vegetation of Arno atoll were not evident in 1952. It is true that brush of small native trees and shrubs tended to grow up in the coconut and breadfruit groves, but the cutting and burning activities of the land-holders kept pace with these threats except in a few places. The encroachment of native secondary forest on the area of poor coconuts of Arno island has been discussed above, but the invasion did not appear to be strikingly rapid.

Special study was made of areas affected by the typhoons of 1905 and 1918. In the area west of Jabu washed out during the typhoon of 1918 (cf. Wells, 1951; fig. 8), Scaevola, Tournefortia, Pandanus, Terminalia, Vigna, Canavalia, Triumfetta, Fimbristylis, Lepturus, Euphorbia, Polypodium, and Cassytha were noted under the young coconut trees. One Scaevola plant growing in a washed-out depression had attained a height of about 16 feet. The Vigna was especially prominent among the herbaceous plants. Its apparent competitive ability in this situation is perhaps not surprising in view of the relatively low nitrogen content of the immature soil (Stone, 1951; profile No. 27).

Walking from Langar island to Ine village I noted young plants of the following species growing in sand deposited since the typhoon of 1905 devastated much of the eastern part of Arno atoll: Cocos, Scaevola, Calophyllum, Pandanus, Guettarda, Tournefortia, Lepturus, Vigna, Triumfetta, Fimbristylis, Wedelia. In most places, the sand which had drifted in between parallel ridges of beachrock representing the shore lines of former islands was devoid of vegetation. Yet it was possible to walk the entire distance from Langar to the southern end of Aljatuen Matolen

on dry land at mid and high tide. Primary succession undoubtedly takes place, but it is apparently a slow process in such situations.

Pemphis acidula, however, was especially abundant along the lagoon shores of this devastated strip. Plants of all sizes up to low trees 15 to 20 feet tall were observed growing on the solid beach rock. Shallow pockets in the rock in which small quantities of sand had accumulated were the seedbeds of this hardy plant. Scaevola frutescens and sprouting coconuts formed thickets along some of the high boulder ramparts behind the shrubbery of Pemphis. Ubiquitous was a black blue-green alga which covered completely the rock fragments of boulder ramparts in exposed situations.

Further confirmation of the hypothesis that vegetational change was slow at Arno in 1952 is afforded by the fact that it was possible to use aerial photographs taken in 1944 and 1945 in mapping the vegetation of the atoll. The photographs were repeatedly checked in the field and no discrepancies were noted other than slight changes in land forms. The vegetation of Arno atoll had remained essentially stable for at least 7½ years.

PHOSPHORUS RELATIONS

The atoll habitat, monotonously uniform to superficial observers, is actually striking in its variety. Permanent residents, for example, are well aware of the differences in the abundance of fish and sharks in different situations. On Arno atoll the fishing was especially good off Bikarej island. Although there was an abundance of fish on the ocean reefs near the Takleb pass, spear-fishing there was dangerous because of the great concentration of sharks. The lagoon shores of the windward islands of Arno atoll were often unpleasantly hot because the coconut

plantings to windward cut off the cooling trades. The lagoon shores of Arno island and Ine, on the other hand, were for the most part plesantly cool, for the trade winds impinged on the villages along their lagoon shores after an uninterrupted sweep across the broad lagoon. Mason (1952) discussed the striking cultural differences to be found on the different islands of Arno atoll. I found that almost every island had a local "wonder" or legend associated with it. The atoll was in effect a microcosm.

Marked differences in the habitats available to plants were also found. Soils varied in texture from peats and mucks through sandy loams to materials composed chiefly of stones and cobbles. Some soils, like those of high, windswept dunes, appeared excessively drained, but elsewhere fresh-water swamps were encountered. The salinity of the ground water varied over a 2,000-fold range, and this variation was reflected in the vegetation. Breadfruit and yaraj plantings were limited to areas of relatively low salinity.

The variation in concentration of readily extractable phosphorus in the soils of Arno atoll was especially noteworthy. Stone reported only 10 pounds per acre in the area of poor coconuts on Arno island, but 860 pounds per acre at one locality on Namwi island. Concentrations in the mangrove peats of Langar island reached 1600 pounds per acre.

Local concentrations of phosphates and phosphatic limestone at Arno were often correlated with present concentrations of roosting and nesting seabirds. The mangrove swamps of Langar and Tinak harbored large colonies of fish-eating terns, the droppings of which are believed to be rich sources of phosphates. Takleb and Namwi islands, formerly Marshallese bird reservations, had local deposits of phosphatic sand and rock.

Although unconsolidated phosphatic sands were commonly encountered in areas of native forest dominated by Ochrosia, Guettarda, Intsia, Barringtonia, or Hernandia, consolidated phosphatic limestone was apparently restricted to those areas of native forest in which Pisonia grandis was or clearly formerly had been the primary species. On Takleb island, for example, phosphatic rock was found only on the part of the island on which grew 3 large Pisonia trees, probably relicts of the former native forest. In order to study this phosphatic soil the author excavated a deep pit near the largest of the Pisonia trees. The profile was: 0 - 2 inches, but extending to a depth of 17 inches in fissures in the phosphatic rock: Black greasy humus with Pisonia roots. Crumb structure well developed when dry. Mucky when wet.
2 - 13 inches, but commonly outcropping at surface and in places continuing to depths of 24 inches: Brown phosphatic limestone. The rock was highly brittle, much fissured, and pockets of unconsolidated phosphatic sand were present.
13 - 22 inches: Pink coral and foram sand with vertical brown phosphatic streaks and fragments of brown phosphatic rock. Grading into
22 - 52 inches: pink coral and foram sand, gradually increasing in coarseness of texture with depth, and containing near the bottom of pit well preserved fragments of branched corals.

This soil apparently developed on a parent material of coral-and-foram sand similar to that found in the 22-52 inch horizon. Phosphatic salts from bird droppings moved downward from the humus layer into the lime sands beneath, combining with these to form insoluble calcium phosphate. Movement downward of the phosphatic salts was effectively

limited to the upper 22 inches of soil by the filter of lime sands. Gradually a matrix of calcium phosphate formed around the grains of limesand, cementing them into solid chunks of rock. The mucky phosphatic humus washed down into the interstices of this rock, in places preventing the further downward movement of materials. Around the largest of the Pisonia trees stood 3 pools of water an inch or two deep, which served as wallows for the numerous pigs of Takleb island. One of these wallows was situated only 11 feet from the soil pit described above. Standing water remained in this wallow at the end of a 36-hour rainless period, whereas no water was encountered in the pit at a depth of 52 inches. Evidently this phosphatic hardpan was capable of perching a water table.

A fragment of rock removed during the excavation of the soil pit was suggestive of the length of time necessary for the formation of the hardpan One side contained a semi-cylindrical cavity approximately 2 inches in diameter. The rock was hardest and darkest around the cavity, which apparently had once been occupied by the root of a tree. It is suggested that the rock must have formed around the root after the latter had attained a diameter of 2 inches, for had the root penetrated the rock after the latter had formed, it surely would have shattered the brittle rock during its increase in diameter. Further, the rock must have formed around the root while the latter was still alive or only recently dead. Coarse, unconsolidated sand would quickly have filled in the cavity left by the decaying root had the latter rotted before the rock was formed. This suggests that the phosphatic rock formed very rapidly, perhaps within less than 100 years, although the length of life of the root of an unknown species of tree under the conditions described is of course not known.

Felix J., the magistrate of Arno atoll, whose family holds land rights on Takleb, stated that the phosphatic rock was first noted in 1905. The island was first settled in 1886, and certain crops not observed on the atoll in 1952 -- the pineapple, tomato, and watermelon -- were grown on the fertile Takleb soils until the development or exposure of the rock made their culture difficult or impossible. It is possible that the removal of the wild trees tended to have a dessicating effect on the soils. During periods of drought the soil may have been exposed to the dire direct rays of the tropical sun, and the resultant "baking" may have accelerated the formation of phosphatic rock. On the other hand, removal of the trees may have been followed by heavy erosion during the torrential downpours so characteristic of Arno atoll. The mucky layer of phosphatic humus, in which the crops were grown, may simply have washed away, exposing the previously formed phosphatic limestone beneath.

For the most part, productive coconut trees occurred on soils of intermediate concentrations of phosphates: 80 to 120 pounds per acre according to Stone's analysis. Although coconuts were successful on these soils, the special crops -- tomatoes, watermelons, pineapples -- in general were not. In 1952 Kapok trees had been successfully introduced only on Takleb. They were stated to have failed on Ine.

On soils of very low concentrations of readily extractable phosphorus even the coconut did poorly. In the interior of Arno island (Fig. 13) where Stone's analysis showed only 10 pounds of readily extractable phosphorus per acre in the surface 6 inches of the soil, was an area of poor coconuts ("laora") forming a semicircular belt around an area of secondary forest. Coconuts observed in clearings of the latter exhibited

the same symptoms as those in the area of poor coconuts adjacent to the secondary forest. It is therefore probable that the condition responsible for the poor growth of coconuts was present throughout the secondary forest. Combined, the two areas totaled 136.6 acres.

Poor coconuts of the "laora" type were also observed by the author in the interior of the widest island of Ebon atoll, in the southern Marshalls. The soil, of which samples were sent to Dr. Stone for analysis, was apparently of the Arno series. On both sides of this area of poor coconuts but no nearer the lagoon were groves of healthy, productive trees growing on phosphatic soils. These local phosphatic deposits, neither of which was larger than 10 acres in extent, had been mined by the Japanese until United States bombers destroyed the loading facilities; about 50,000 tons were removed. The author excavated a small soil pit in an area undisturbed by mining operations. A highly organic, fine-textured layer 8 inches thick covered 8 inches of gray sand, which in turn lay over solid, hard phosphatic limestone, through which it was impossible to dig with a hand shovel. The formation was apparently thick, however, for the Japanese excavations had pierced the water table and created a fresh-water pond perhaps 1000 square feet in area.

To summarize, "Laora" is a disease of coconuts occurring in the interiors of the wider islands of atolls on soils of low concentrations of readily extractable phosphorus. On local phosphate deposits in the interiors of one such wide island the coconut trees were healthy and productive, whereas the palms on an adjacent, non-phosphatic area were not thrifty. The sites were apparently identical in all respects with the exception of the difference in phosphate concentration of the soil.

The presence or absence of local phosphate deposits in the interiors of wide islands is probably not fortuitous. At Arno the tops of large Pisonia trees were invariably crowded with flocks of roosting and nesting seabirds. In fact, the birds appeared to "prefer" the branches of the Pisonia to those of any other tree. The droppings of these myriads of birds would eventually result in the formation of phosphatic rock, as observed on Takleb island. Like many of the native trees of the southern Marshalls, Pisonia grandis tends to occur in groves -- that is, in pure stands less than 10 acres in size. Present local deposits of phosphatic rock may well coincide with former Pisonia groves.

The Marshallese voyagers, upon arriving at a new atoll, probably cleared first the forests of the wider islands. In the interiors of these islands the ground water was sufficiently fresh to permit the growth of their basic crops, breadfruit and yaraj. At Arno island yaraj pits and abandoned housesites were concentrated in the interior; it is probable that this interior land has had a longer history of continuous human use than any other area of the atoll. From the time it was first cleared until 1952 -- at least 220 years and probably much longer -- large flocks of fish-eating seabirds were absent, for the birds tended to avoid villages, where they were persecuted. Consequently, any large-scale deposition of phosphates by seabirds effectively ceased in the interior of Arno island with the arrival and establishment of the Marshallese voyagers. It is perhaps not surprising that after centuries of cropping and leaching losses some of these soils were not able to supply the coconut tree with sufficient phosphorus to meet its needs.

According to the data of Walker (1906), a ripe coconut minus the husk and shell contains 1.911 gr. phosphoric acid (P_2O_5). On the average about 1850 nuts per acre of coconut land were converted into copra on Arno atoll in 1951. This is about 3.4 pounds of phosphorus (P) removed per acre in copra. In addition about 0.8 pounds of phosphorus was removed from coconut plantations in the shells of the husked nuts, making a total of 4.2 pounds per acre. About 3.8 tons of phosphorus were lost to the atoll in 1951 in the export of copra. The shells, of course, were not exported but were used as fuel locally. Using the data of Bachofen (Anonymous, 1900) the amount of phosphorus lost to the atoll in 1951 in the export of copra drops to 1.37 tons; the loss per acre becomes 1.3 pounds. Of course, in order to arrive at a more accurate estimate it would be necessary to analyze Arno coconuts or copra. The data are merely intended to indicate the order of magnitude of the cropping loss. Indeed, with the abandonment of the unproductive groves and the establishment of secondary forest, the early stages of a shifting agriculture were present in 1952. Only the establishment of Pisonia groves and rookeries within the secondary forest were necessary to complete the cycle. It would thus appear that the cycle of movement of phosphorus from sea to land and back is of considerable importance in the agriculture and ecology of inhabited atolls in the southern Marshalls. I believe that a careful geochemical study of the phosphorus cycle on inhabited coral atolls would be of considerable general interest, for it would combine the work of the chemist, the soils scientist, the geologist, the ichthyologist, the ornithologist, the botanist-agriculturist, and the anthropologist in the investigation of a vital phase of the economy of atolls.

1. Before the arrival of the Marshallese voyagers, the vegetation of Arno atoll was composed chiefly of dicotyledonous trees and shrubs. Along boulder ramparts and extending perhaps 100 feet inland on windward islands was a scrub vegetation composed principally of Scaevola frutescens but also including Tournefortia argentea, Pandanus tectorius, Terminalia samoensis, and Guettarda speciosa. This scrub merged inland on stony soils with a forest of trees 20 to 60 feet tall. Prominent among these were Barringtonia asiatica, Hernandia sonora, Ochrosia oppositifolia, Intsia bijuga, Pandanus tectorius, Guettarda speciosa, Pisonia grandis, and Cordia subcordata. Ground cover was sparse, being featured chiefly by tree seedlings and suckers, clumps of Asplenium nidus among the rocks, and patches of Peperomia sp. On sandier soils nearer the lagoon, groves of tall Pisonia trees served as rookeries for numerous fish-eating seabirds. Hardpans of phosphatic limestones developed under the Pisonias. Allophylus timorensis, Guettarda speciosa, Intsia bijuga, Pipturus argenteus, Cordia subcordata, and Premna obtusifolia were also present on sandy interiors, although they probably did not form mixed stands with the Pisonias. Along the dunes of lagoon shores a scrub of Scaevola with occasional Suriana maritima and Sophora tomentosa formed a narrow belt at the edge of the forest. Along eroding lagoon shorelines in which beachrock was exposed, Pemphis acidula formed the bulk of the vegetation.

Saline flats were covered with nearly pure stands of Pemphis. Saline swamps may have been occupied by a vegetation of mangrove trees, although it is possible that these were introduced later by the Marshallese.

Fresh-water swamps were covered by forests of Pandanus tectorius.

Along the lagoon shores of island damaged by typhoons herbaceous plants such as Triumfetta procumbens, Lepturus repens, Wedelia biflora, Vigna marina, Fleurya ruderalis, and Fimbristylis atollensis maintained precarious footholds in the face of the advancing woody vegetation.

2. The arrival of the Marshallese settlers introduced a period of major change in the vegetation. The forests of the sandy interiors of islands were partially cleared, yaraj pits dug and cultivated, and breadfruit and coconut trees planted. Perhaps 15 percent of the land area of the atoll was given over to agriculture. Breadfruit groves flourished in the interiors of the wide islands and coconut trees lined their lagoon shores.

3. Housesites in the interior of Arno island were abandoned in the middle of the 19th century after having been occupied for at least 120 and perhaps 300 or more years. An Hawaiian mission was established at Ine in 1873, marking the first recorded date in Arno's history. In 1876 Iroij Lekaman removed the restrictions on colonization of the only two sizeable islands of Arno atoll - Takleb and Namwi -- on which the native vegetation remained unaltered or nearly so; much of the native forest was removed to make way for breadfruits, coconuts, and other crops. Germany established a protectorate over the Marshall Islands in 1885. German administrators and traders encouraged the production of copra. Pigs were introduced.

4. During the early part of the 20th century the acreage under coconuts increased rapidly at the expense of the native scrub and forest. Native herbs, however, prospered in the new habitat. Pigs devastated the yaraj pits and uprooted Tacca plants in the coconut groves. The breadfruit groves of the interior of Arno island with their yaraj pits were abandoned,

and a native forest of Allophylus, Guettarda, Premna, and Pandanus developed in which certain varieties of breadfruit persisted as scattered trees, reproducing by root suckers and seeds. A typhoon did serious damage to the islands of the eastern part of the atoll in 1905.

5. Soon after the beginning of the first World War the Japanese replaced the Germans as administrators of the Marshall Islands. The Marshallese were encouraged to purchase Japanese exports, especially rice. A destructive typhoon hit Arno atoll in 1918, washing out parts of islands and uprooting trees. Japanese agriculturists advised the Marshallese to increase their coconut plantings. Plantations were unsuccessful, however, in the interior of Arno island on the lands surrounding the site of the ancient village. Copra production in the Marshall Islands probably reached a maximum under the Japanese.

6. In 1944 Kwajalein, Majuro, and Eniwetok were occupied by armed forces of the United States. Although the copra trade was disrupted, Arno was not the scene of major military activity. Aerial photographs taken in 1944 and 1945 revealed that about 69 percent of the land area of Arno atoll was under coconut trees. This area had not changed appreciably by 1952. Native forest and scrub were restricted chiefly to stony land and the ocean sides of windward islands. By 1951 copra production had increased to an output of 622 tons, but secondary forest continued to encroach on the area of poor coconuts of Arno island. Dry land was exposed at mid or high tide the entire length of the eastern part of Arno atoll from Langar island to Aljatuen Matolen, but plant colonization on the newly formed land was slow. Pemphis acidula, however,

had succeeded in establishing itself in large numbers on the exposed beach rock of the lagoon shore of this region and Scaevola bushes grew along the high boulder ramparts.

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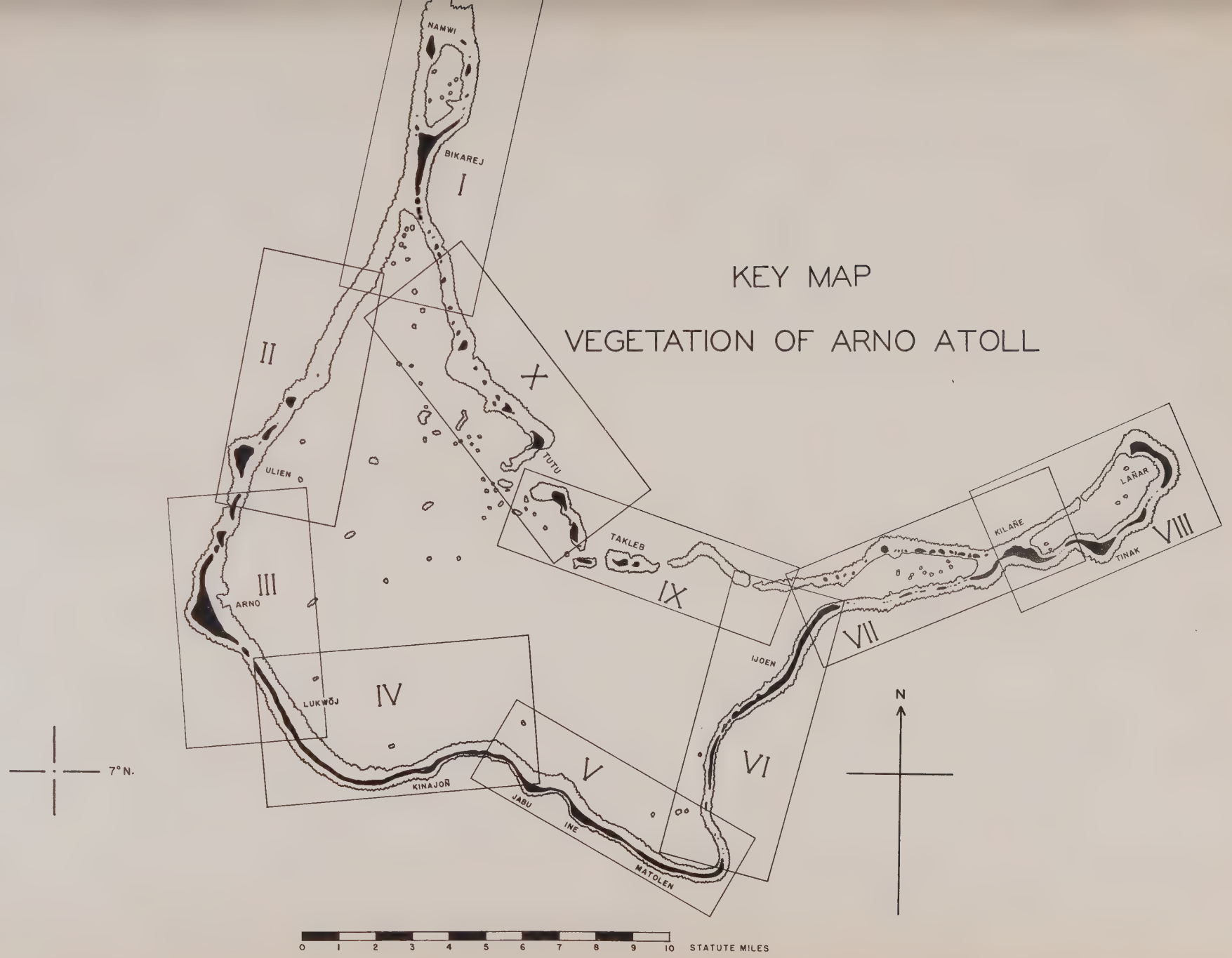

KEY MAP
VEGETATION OF ARNO ATOLL
NAMWI
BIKAREJ
I
II
X
ULIEN
TUTU
TAKLEB
IX
III
ARNO
KILAÑE
LAÑAR
TINAK
VIII
VII
IJOEN
IV
LUKWŌJ
V
VI
KINAJOR
JABU
INE
MATOLEN
7° N.
N
0 1 2 3 4 5 6 7 8 9 10 STATUTE MILES

FIGURE I

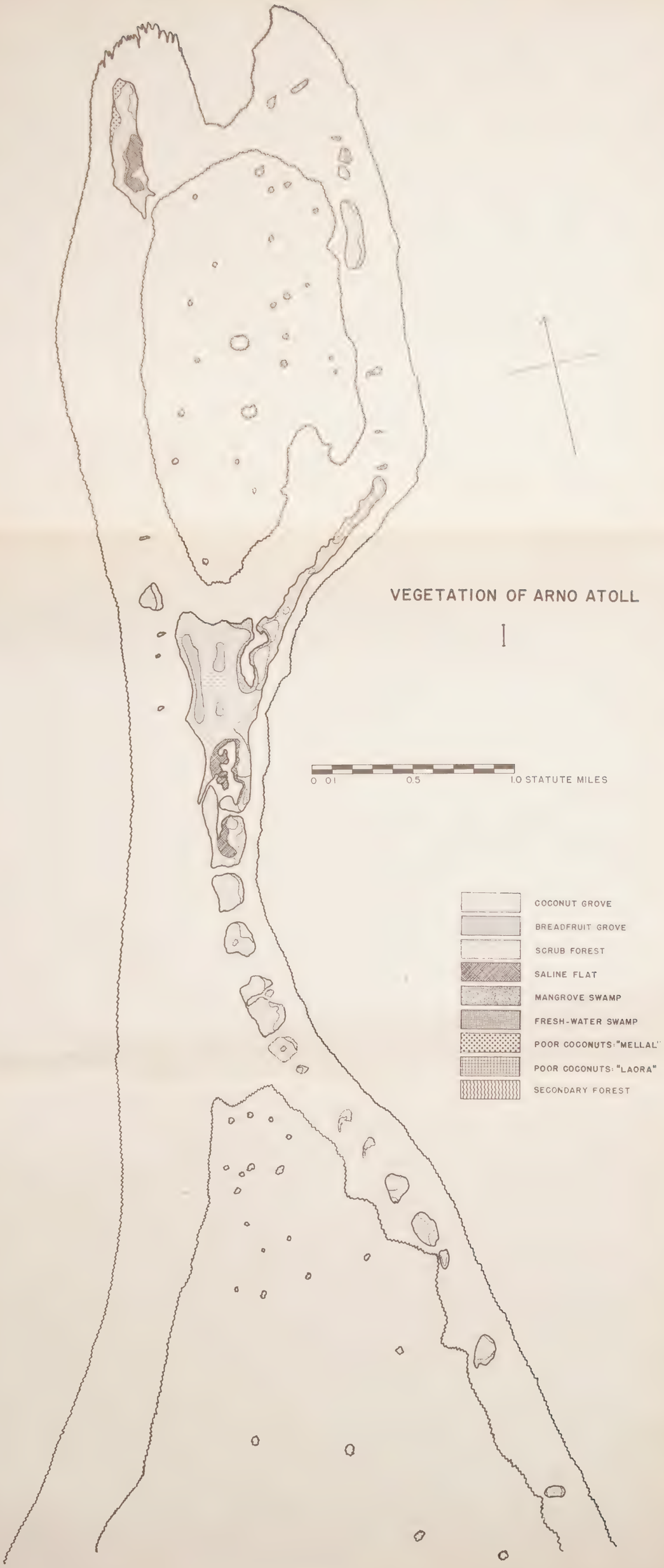

VEGETATION OF ARNO ATOLL
0 0.1 0.5 1.0 STATUTE MILES
COCONUT GROVE
BREADFRUIT GROVE
SCRUB FOREST
SALINE FLAT
MANGROVE SWAMP
FRESH-WATER SWAMP
POOR COCONUTS: "MELLAL"
POOR COCONUTS: "LAORA"
SECONDARY FOREST

FIGURE 2

COCONUT GROVE
BREADFRUIT GROVE
SCRUB FOREST
SALINE FLAT
MANGROVE SWAMP
FRESH-WATER SWAMP
POOR COCONUTS: "MELLAL"
POOR COCONUTS: "LAORA"
SECONDARY FOREST
VEGETATION OF ARNO ATOLL
II
0 0.1 0.5 1.0 STATUTE MILES

FIGURE 3

VEGETATION OF ARNO ATOLL
III
0 01 05 1.0 STATUTE MILES
COCONUT GROVE
BREADFRUIT GROVE
SCRUB FOREST
SALINE FLAT
MANGROVE SWAMP
FRESH-WATER SWAMP
POOR COCONUTS: "MELLAL"
POOR COCONUTS: "LAORA"
SECONDARY FOREST

FIGURE 4

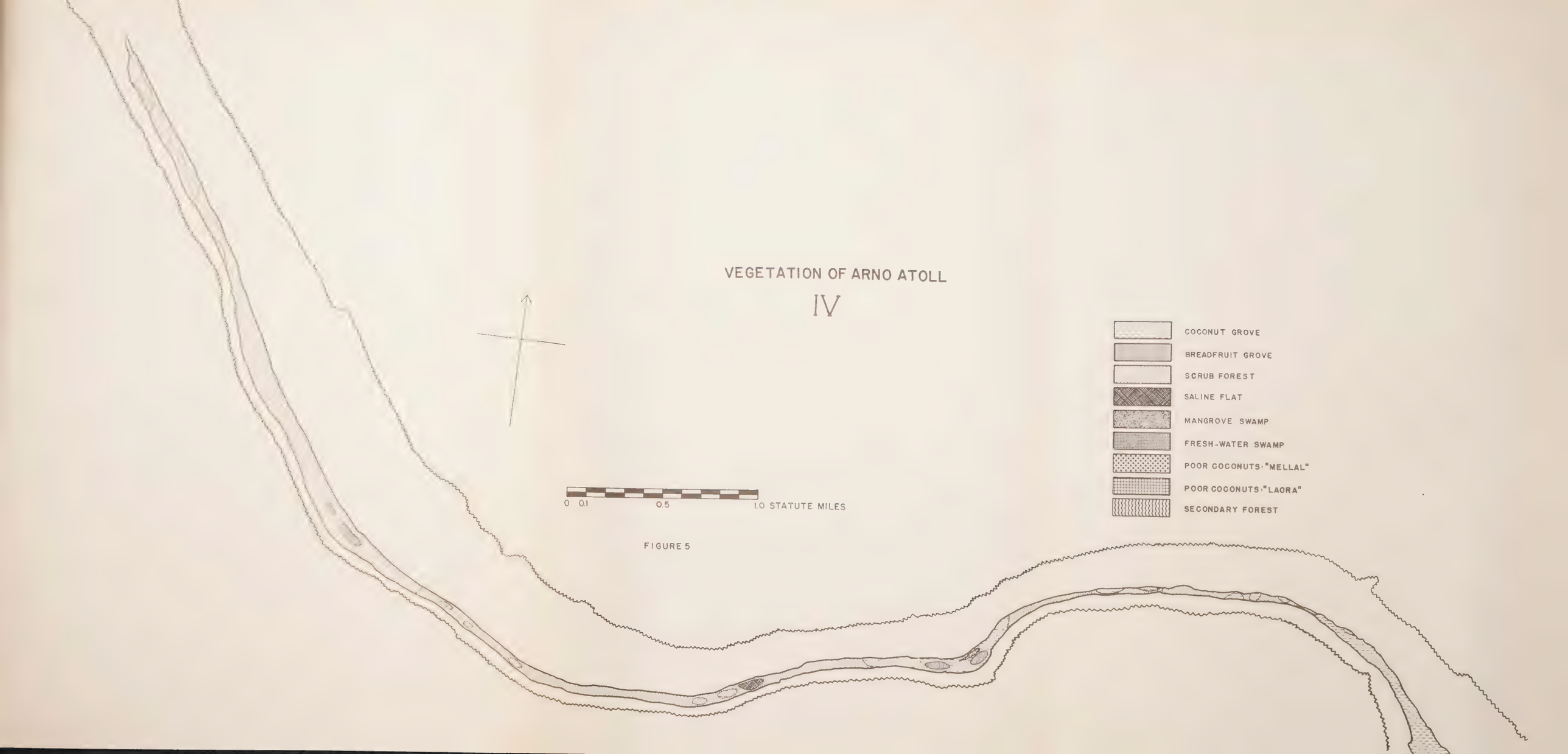

VEGETATION OF ARNO ATOLL
IV
COCONUT GROVE
BREADFRUIT GROVE
SCRUB FOREST
SALINE FLAT
MANGROVE SWAMP
FRESH-WATER SWAMP
POOR COCONUTS: "MELLAL"
POOR COCONUTS: "LAORA"
SECONDARY FOREST
0 0.1 0.5 1.0 STATUTE MILES

FIGURE 5

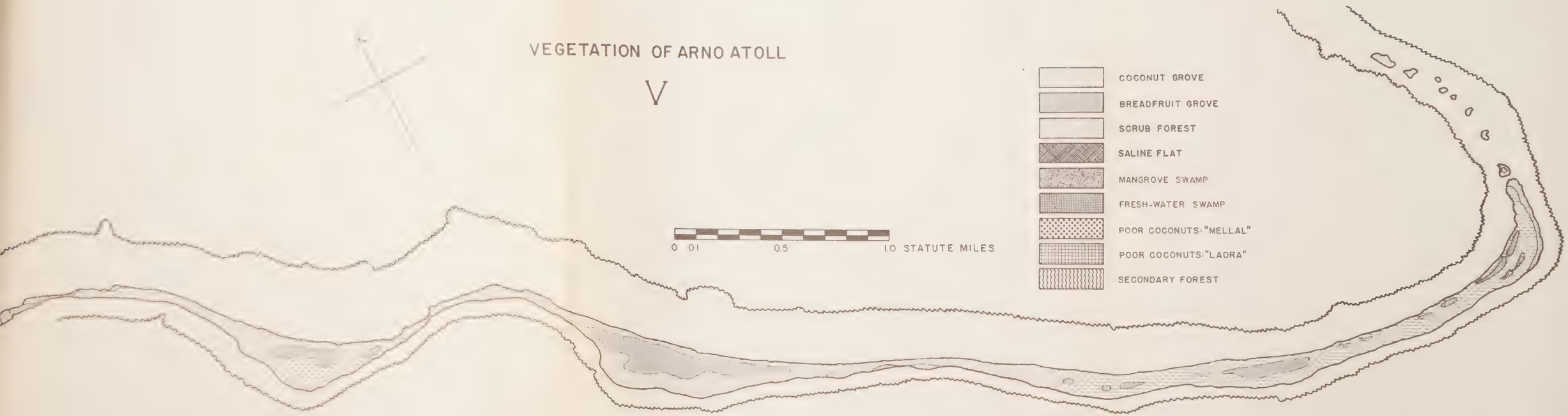

VEGETATION OF ARNO ATOLL
V
0 0.1 0.5 1.0 STATUTE MILES
COCONUT GROVE
BREADFRUIT GROVE
SCRUB FOREST
SALINE FLAT
MANGROVE SWAMP
FRESH-WATER SWAMP
POOR COCONUTS: "MELLAL"
POOR COCONUTS: "LAORA"
SECONDARY FOREST

FIGURE 6

VEGETATION OF ARNO ATOLL
VI
COCONUT GROVE
BREADFRUIT GROVE
SCRUB FOREST
SALINE FLAT
MANGROVE SWAMP
FRESH-WATER SWAMP
POOR COCONUTS: "MELLAL"
POOR COCONUTS: "LAORA"
SECONDARY FOREST
0 0.1 0.5 1.0 STATUTE MILES

FIGURE 7

VEGETATION OF ARNO ATOLL
VII
COCONUT GROVE
BREADFRUIT GROVE
SCRUB FOREST
SALINE FLAT
MANGROVE SWAMP
FRESH-WATER SWAMP
POOR COCONUTS: "MELLAL"
POOR COCONUTS: "LAORA"
SECONDARY FOREST
0 01 05 1.0 STATUTE MILES

FIGURE 8

VEGETATION OF ARNO ATOLL

VIII

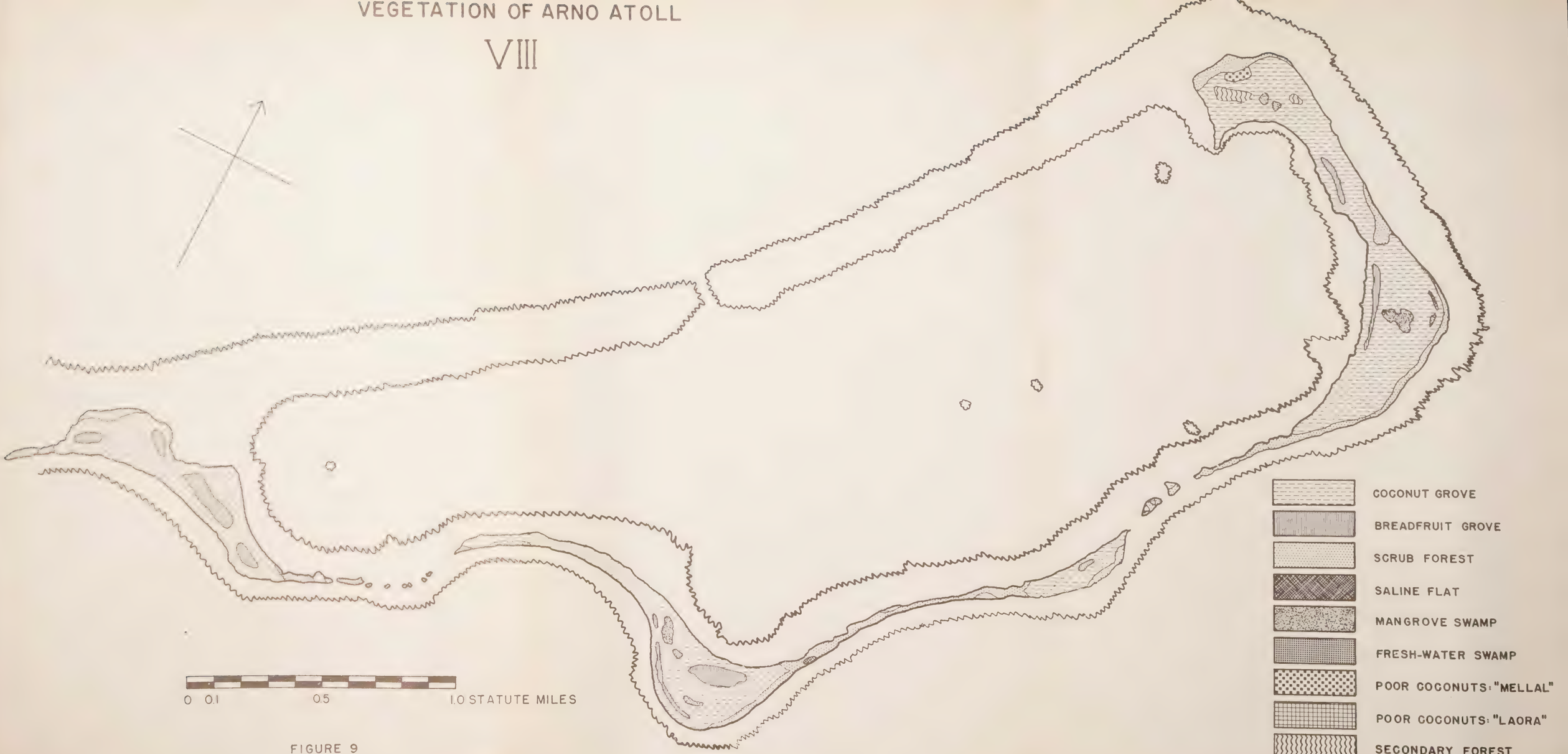


FIGURE 9

VEGETATION OF ARNO ATOLL

IX

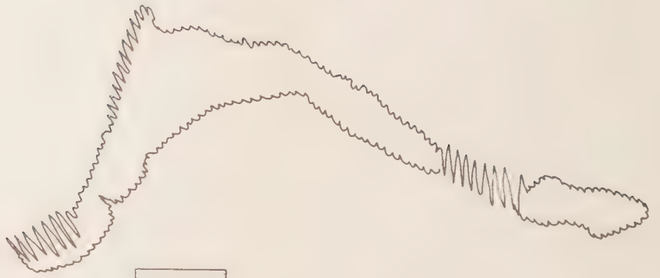
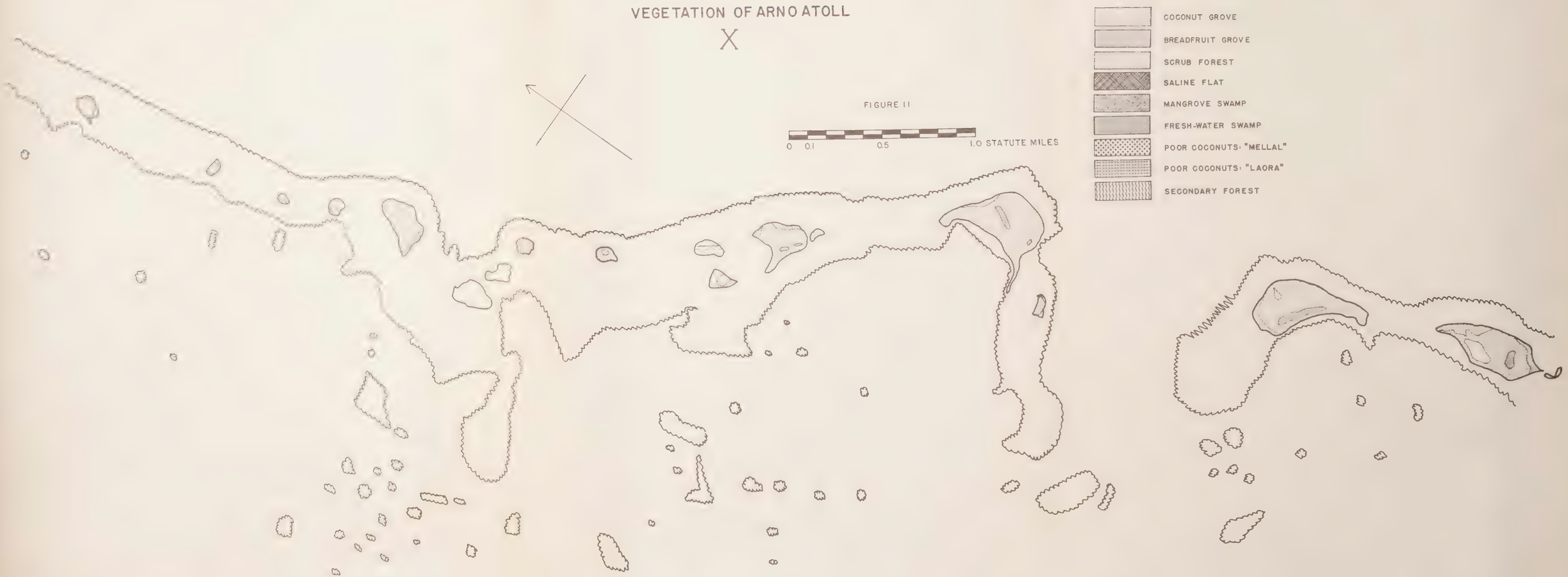


FIGURE 10


VEGETATION OF ARNO ATOLL
X
FIGURE 11
0 0.1 0.5 1.0 STATUTE MILES
COCONUT GROVE
BREADFRUIT GROVE
SCRUB FOREST
SALINE FLAT
MANGROVE SWAMP
FRESH-WATER SWAMP
POOR COCONUTS: "MELLAL"
POOR COCONUTS: "LAORA"
SECONDARY FOREST

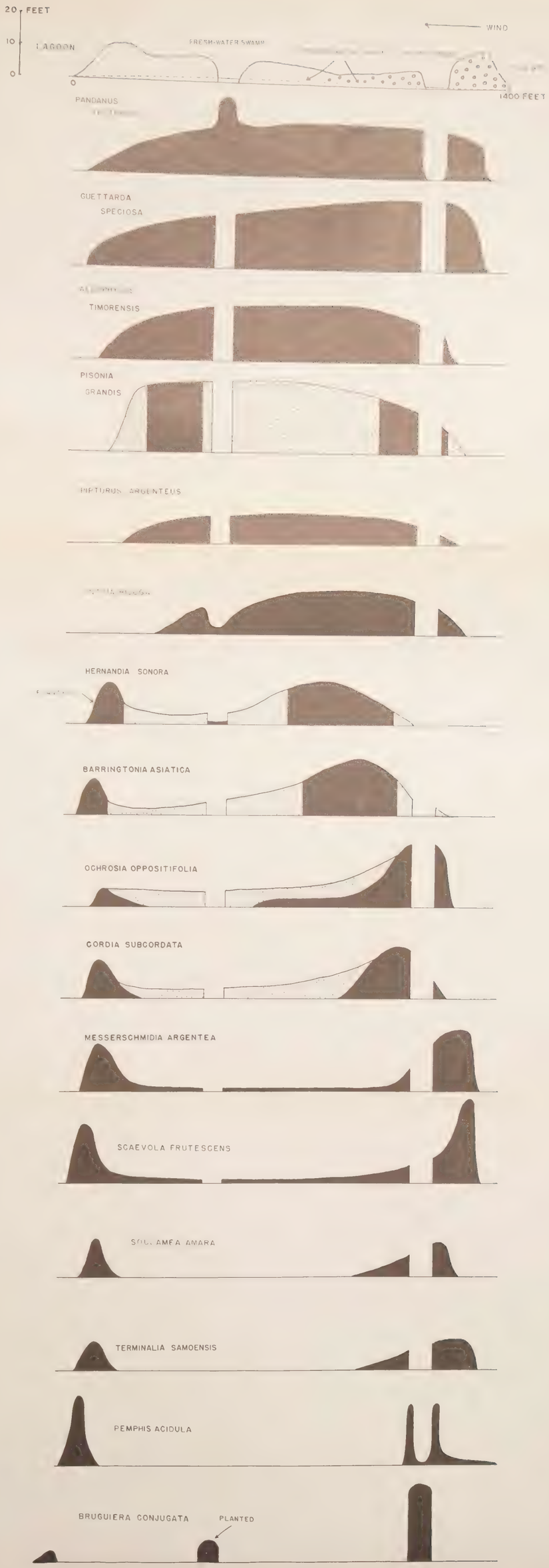


FIGURE 12. DISTRIBUTION AND IMPORTANCE OF CERTAIN NATIVE TREES.
(EXPLANATION IN TEXT)

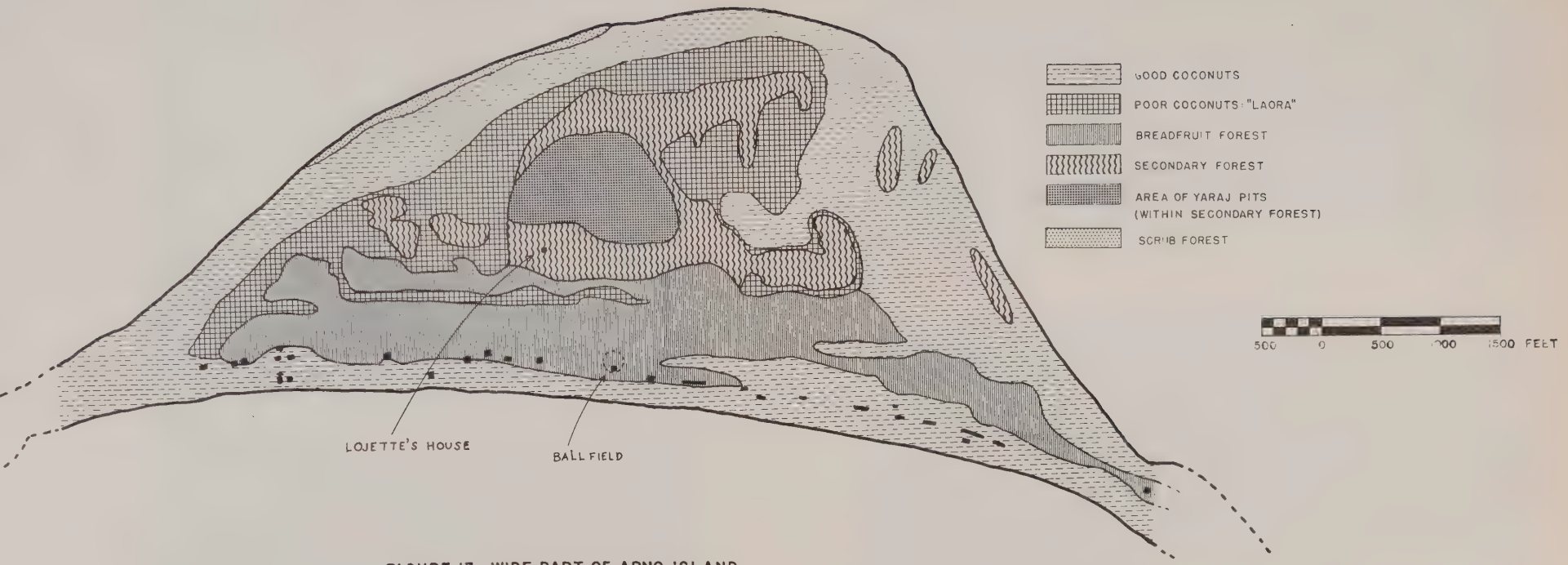


FIGURE 13. WIDE PART OF ARNO ISLAND

Fig. 14. Productive Coconut grove. Ine. 8/23/52.

Fig. 15. Poor Coconuts ("Laora"). Arno Island. Nearly half the palms are dead. 7/15/52.

Fig. 16. Breadfruit grove. Ine. Ground layer is dense in open groves. 8/23/52.

Fig. 17. Yaraj pit, Ebon island, Ebon atoll. 9/20/52.

Fig. 18. Guettarda on stony land near rampart. Langar island. 8/15/52

Fig. 19. Ochrosia stand on stony land, Bikarej island. The trees are about 40 feet tall. 7/25/52.

Fig. 20. Barringtonia stand, stony land, Langar island. 8/15/52.

Fig. 21. Large Pisonia tree, Takleb island. Tree was 28.4 feet in circumference and 80 feet tall. Note numerous suckers. 8/5/52.

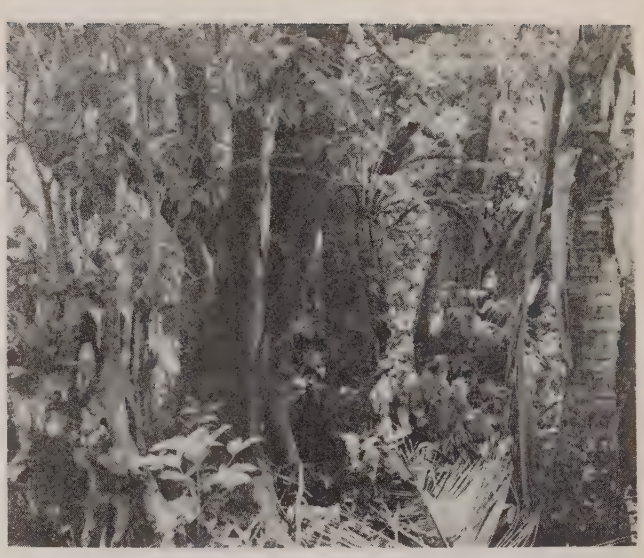


Fig. 22. Pisonia trees, Takleb island. The trees have originated from sprouts along a single fallen log, the remains of the roots of which are visible at left. 8/5/52.

Fig. 23. Mangrove swamp. Compare forms of old trees at right with straight young poles on left. Langar island. 8/15/52.

Fig. 24. Fresh-water swamp. The stand consists chiefly of Pandanus tectorius. Ulien island. 7/16/52.

Fig. 25. Fresh-water pond and swamp. The water was about 24 inches deep when photographed. Ulien island. 7/16/52.

Fig. 26. Secondary forest. Rank growth of Pandanus tectorius in abandoned yaraj pit. Arno island. 7/15/52

Fig. 27. Modern house. Note gravel courtyard around house. Arno island. 8/20/52.

Fig. 28. Gravel in modern courtyard. Arno island. 8/20/52.

Fig. 29. Gravel in courtyard of abandoned housesite. Near yaraj pits, Arno island. 7/15/52.